Interim report
The Tuolumne River below Hetch Hetchy Reservoir: Characterization of the benthic macroinvertebrate assemblage in the river and Poopenaut pond and response of benthos and drift to experimental spring release events

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Introduction

Although the 100-meter-tall O'Shaughnessy Dam and associated Hetch Hetchy Reservoir are prominent features of Yosemite National Park, the below-dam portions of the Tuolumne River within Yosemite National Park remain something of an ecological frontier. The Poopenaut Valley reach of the river (including Yosemite National Park Planning Segment 5 and part of Segment 6) is close to a major road and is accessible by both a maintained hiking trail and a dirt utility road, but travel along the river is cross-country in nature, which likely explains the comparative lack of visitation. This report provides baseline data on the benthic macroinvertebrate (BMI) assemblage in this river reach and the results of an ecosystem scale experiment designed to test the response of the river's biotic and abiotic elements to two spring release events.

Macroinvertebrates are excellent integrators of physical, chemical, and biological processes and are highly valued as indicators (Plafkin et al. 1989, Barbour et al. 1999). Invertebrates are also valuable as indicators because these animals include primary, secondary, tertiary, and higher-level consumers (e.g., Wallace and Hutchens 2000) and in turn are a critical food resource for a variety of vertebrate taxa (Allan 1995).

Dams can cause downstream perturbations as a function of reduced and altered river flow, increased water clarity, scouring, and altered temperature regime (Ward 1984, Allan 1995, Bowen et al. 2003, Dewson et al. 2007), and ecological effects can cascade throughout the food web and up and down the river corridor (e.g., Holmquist et al. 1998, McIntosh et al. 2002, Greathouse et al. 2006a, b, Sabo et al. 2010). There can be a reduction of macroinvertebrate species richness, and an increase in abundance, below dams (Stanford and Ward 1989, Allan 1995), although this relationship can be altered if migratory fauna make up a large proportion of the assemblage (Holmquist et al. 1998). Lowest species richness is typically found in the tailwaters just below an impoundment (Stanford and Ward 1989, Armitage and Blackburn 1990). Replacement of certain taxa by others is common; for instance, low flows often result in a reduction of more lotic mayfly taxa and an increase in more lentic taxa (Brittain and Saltveit 1989). 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. 2007). Further, extant habitat tends to be more fragmented when flow is reduced (Lake 2000, but see Englund and Malmqvist 1996). There are often losses due to drift associated with flow spates (Waters 1972, Imbert and Perry 2000, Mochizuki et al. 2008) or flow reduction (Minshall and Winger 1968, Canton et al. 1984, Dewson et al. 2007). Loss of habitat quantity associated with flow reductions may be as important as loss of habitat quality in structuring invertebrate assemblages (Englund and Malmqvist 1996, Waddle and Holmquist submitted), and flow reductions can disrupt floodplain connectivity (Bunn and Arthington 2002, Bowen et al. 2003).

Large experimental or flushing flows have been used increasingly as experiments designed to both better understand effects of river regulation and to improve physical and ecological integrity of regulated rivers (Stanford et al. 1996, Poff et al. 1997, Michener and Haeuber 1998). The experimental release initiative at Glen Canyon/Lake Powell (Andrews and Pizzi 2000, Shannon et al. 2001) was a high profile example of this approach.

Drift of benthic macroinvertebrates is important in structuring stream assemblages (Waters 1972, Wallace 1990). Both reductions and increases in flow can enhance drift (Waters 1972, Scullion and Sinton 1983, Perry and Perry 1986), and altered drift patterns can therefore occur below dams and in other regulated systems (Irvine and Henriques 1984, Holmquist et al. 1998, Imbert and Perry 2000, Greathouse et al. 2006b). For instance, loss of taxa below dams may occur, because drift losses are not replenished by drifting individuals from upstream reaches, which are often trapped in the reservoir. In turn, drift from the reach immediately below a dam may not be carried very far downstream because of reduced flows.

Seasonal wetlands perched above the river were historically inundated seasonally and almost certainly contributed significant macroinvertebrate biodiversity to the river corridor. Ponds, marshes, and wet meadows harbor large and diverse aquatic faunas (Wiggins et al. 1980, Law and Morton 1993, Williams 2006) that change throughout the dry-wet-dry progression in the Sierra, at least in higher elevation systems, further enhancing diversity (Holmquist and Schmidt-Gengenbach 2006, Holmquist et al. 2010, submitted) and food resources available to vertebrates (Batzer and Wissinger 1996).

For the first year of study, the goal was to develop an understanding of current riffle assemblage structure in this reach of the Tuolumne River. To this end, we conducted spatially and temporally extensive sampling designed to capture year-round variability and to include as many taxa as possible. The second and third years of study assessed the effects of spring releases on the BMI assemblage. During the fourth year of study we 1) examined BMI drift response to artificial flow spates and reductions, and

2) characterized the invertebrate assemblage in the Poopenaut Pond, which forms in response to both natural and engineered phenomena in the Tuolumne watershed. We examined not only the aquatic drift, as is mostly commonly done, but also the terrestrial fauna that were entrained in the water column.

Methods

Assemblage Structure

We sampled the river at approximately six-week intervals from spring of 2007 through winter of 2008, sampling at a different randomly-chosen location on each trip (Table 1, Fig. 1-5). We sampled benthic macroinvertebrates, took a variety of physical measurements, and made habitat assessments at each of these stations.

In an effort to ensure comparability with other ongoing sampling in the Tuolumne River, and at the request of the City, we used the US Environmental Protection Agency rapid bioassessment protocols (Barbour et al. 1999). These protocols emphasize kick netting in cobble, but generally not sand, habitats (Plafkin et al. 1989, Barbour et al. 1999). The net (with 0.5mm mesh) was held perpendicular to the current, and the upstream substrate was disturbed by vigorously kicking, scraping, overturning, and rubbing large cobbles, and small cobbles, gravel, and silt were dislodged and/or suspended, all while the "kicker" was moving upstream. The composite sample was then rinsed and transferred to a vessel and preserved in 70% non-denatured ethanol, cleaning and removing large pieces of gravel, leaves, and twigs in the process. Each sample consisted of four randomly selected $0.5m^2$ subsamples. Although not part of the EPA protocols, we also collected some limited rock scraping samples on large rock

Table 1. Sampling sites, dates, and UTM coordinates (WGS84, Zone 11).

1	21 March 2007	11S 253212mE	4201688mN
2	3 May 2007	11S 254007mE	4202441mN
3	15 June 2007	11S 254023mE	4202150mN
4	27 July 2007	11S 254112mE	4202602mN
5	10 Sept 2007	11S 254200mE	4202804mN
6	22 Oct 2007	11S 252931mE	4201265mN
7	3 Dec 2007	11S 254322mE	4203257mN
8	1 Feb 2008	11S 254451mE	4203285mN

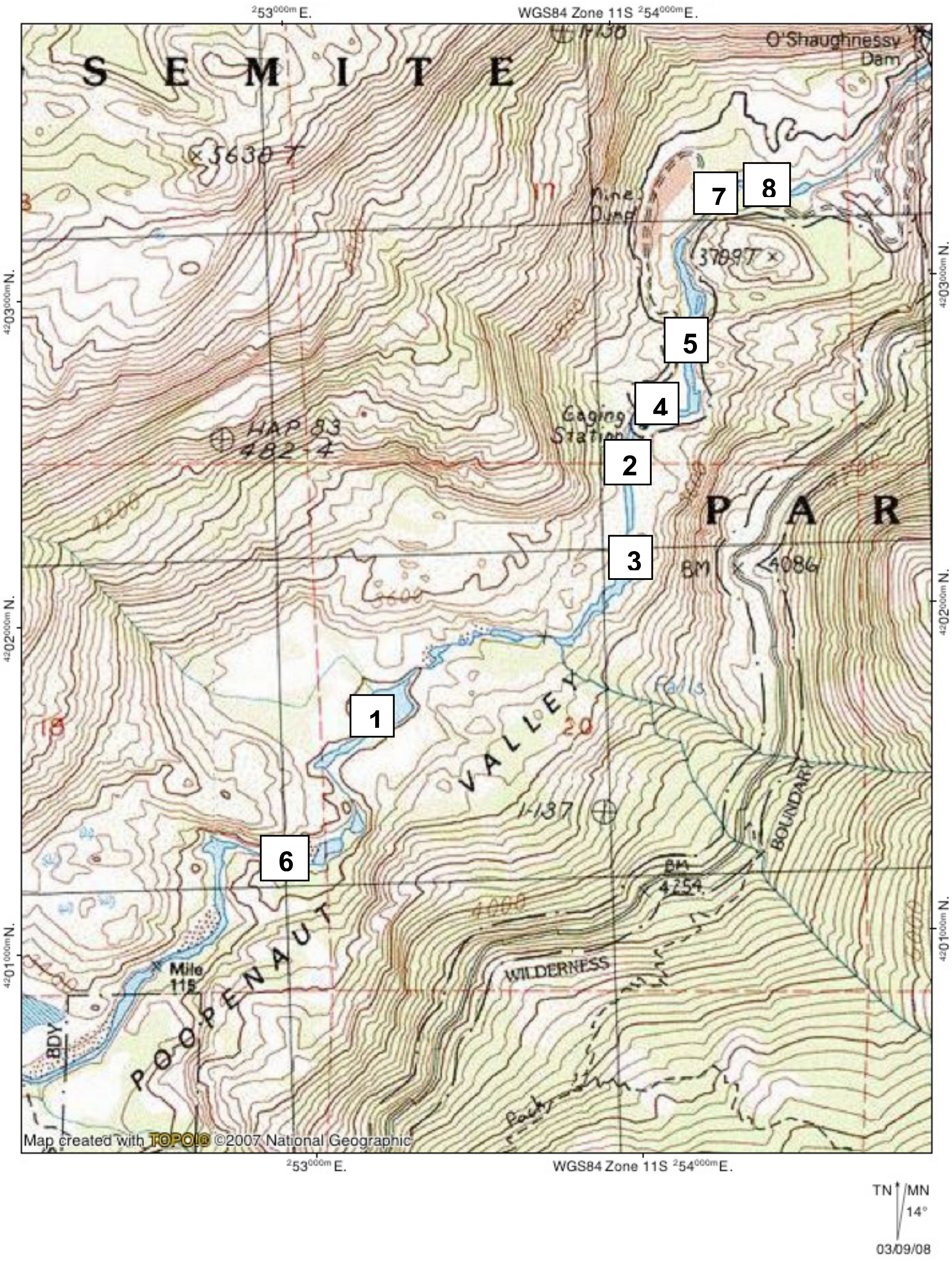

Fig.1. Location of sampling sites.

Fig 2. Sites 1 (top) and 2 (bottom).

Fig. 3. Sites 3 (top) and 4 (bottom).

Fig. 4. Sites 5 (top) and 6 (bottom).

Fig. 5. Sites 7 (top) and 8 (bottom).

substrata (boulders and submerged slabs). Samples were collected in a 0.3x0.3m Surber sampler.

Samples were sorted completely in the lab, rather than subsampled, because complete sorting reduces the variance of metrics and increases taxon richness (Courtemanch 1996, Doberstein et al. 2000). Sorting was particularly laborious due to the large amounts of filamentous green algae that were present (Fig. 2-4). Taxa were identified to the lowest possible level and entered on EPA Benthic Macroinvertebrate Laboratory Bench Sheets. Kerans and Karr (1994) found that richness, dominance, and trophic metrics were the consistently most useful, and our selected metrics reflect these findings. Calculated metrics include individual family and genus/species densities, total individuals/m^2, species and family richness, species and family richness following Margalef's correction for differential abundance (D_{Mg}= (S - 1)/ln N, where S= number of species or families and N= number of individuals; Clifford and Stephenson, 1975, Magurran 2004), percent species and family dominance (single taxon), %Ephemeroptera-Plecoptera-Trichoptera (for both individuals and taxa), relative contributions of all functional feeding groups (singly and in various combinations and ratios), and the Hilsenhoff biotic index (Hilsenhoff 1987, Barbour et al. 1992, Kerans and Karr 1994). The Hilsenhoff index (HBI) is $\Sigma(n_i a_i/N)$, where n_i = number of individuals in the ith taxon, a_i = tolerance value (1-10) assigned to that taxon, and N = total number of individuals in sample with known tolerance values. This index provides an indication of the relative importance of "tolerant' and "intolerant" taxa in an assemblage (those that can and cannot live, respectively, in degraded habitats; tolerant fauna tend to be outcompeted in healthier systems, and "intolerant" taxa predominate). Functional feeding groups are broadly analogous to guilds (Root 1973, Hawkins and MacMahon 1989, Merritt and Cummins 1996). We used Merritt et al. (2008), Aquatic Bioassessment Laboratory (2003), Smith (2001), and Thorp and Covich (2001), among others, as our sources of functional feeding group assignments and Aquatic Bioassessment Laboratory (2003) and Merritt et al. (2008) as our sources for tolerance values. We were able to assign a functional feeding group and a tolerance value for each taxon. The assemblage structure was compared with that found in two other studies using Sorensen's similarity coefficient (S_S= 2a/(2a+b+c), where a= joint occurrences, b= taxa found in group B but not group A, and c= taxa found in group A but not group B; Krebs 1989).

Physical measurements included flow, depth, temperature, stream width, high water mark, percent shade, and coarse estimates of percentages of cobble, gravel, sand, and silt. Flow, depth, temperature, and stream width measurements were made at each of the kick net subsample locations after each subsample was collected, whereas the remainder of the measurements were estimates for the entire site. We measured flow with a General Oceanics rotary flowmeter (with high-speed rotor) on a telescoping wading rod. We took photos and recorded UTM coordinates (WGS84, Zone 11) at each location.

We also completed EPA Habitat Assessment Field Data Sheets (Barbour et al. 1999) at each site at "habitat unit"/reach scales (10-1000m; Frissell et al. 1986, Bauer and Ralph 1999, Fausch et al. 2002). The form includes visual estimates of habitat quality in terms of 1) epifaunal substrate, 2) substrate embeddedness, 3) velocity/depth regime, 4) sediment deposition, 5) channel flow status, 6) channel alteration, 7) frequency of riffles, 8) bank stability, 9) vegetative protection, and 10) width of riparian vegetation zone.

Most metrics demonstrated normality via Lilliefors tests (Lilliefors 1967), although two metrics required removal of an outlier to meet this assumption. Some initial data exploration was done via multiple regressions. Because of potential collinearity in the multiple regression models, p for entry into, or removal from, the models was set at <0.05 and tolerance was set at 0.1.

Although the study was not designed to test seasonal differences, some trends were apparent, and we wished to examine some unplanned contrasts. Some response variables demonstrated heteroscedasticity ($F_{\max}$ and Cochran's tests; Kirk 1982) which for a few variables was not removed by various transformations. We therefore used two-tailed Mann-Whitney U tests for all contrasts. We performed tests for most response variables, so the potential for multiple comparison error should be kept in mind when interpreting these results based on per-contrast error rate. All statistical tests were done in SYSTAT.

Response to Experimental Releases

We sampled the below-dam reach one day before, one day after, and two months after each of the experimental releases described in Chapters 1 and 2 in order to capture pre-release and post-release conditions and to assess initial persistence of any changes induced by the release. We sampled sites 2-5 and 7-8 (Figs. 1-5) at each of these three intervals.

We collected 1m^2 kick net samples as described above, and almost all methodology was identical to the Year 1 assemblage characterization described above. We did not do the ancillary rock scrapings in Years 2 and 3, but we added several additional metrics. A great deal of green algae was collected in the process of kick net sampling, and we used the gram dry mass of these samples as a coarse (under)estimate of algal biomass. Algal material was separated during faunal sorting, and algal samples were dried at 90^o C for 24 hours prior to weighing. We collected water samples from each site, at each visit, for measurement of pH, total dissolved solids, and conductivity in the lab with a Hanna model HI98129 combination meter. We used Hanna HI7031 conductivity calibration solution (1413μS/cm at 25^o C), Orion perpHect buffer 7, (ph 7.00 +/-0.01 at 25^o C), and Hanna HI70300 storage solution. We also measured percent tree canopy cover with a convex spherical densiometer (Lemmon 1956, 1957) manufactured by Forest Densiometers.

We analyzed release effects with 1x2 ANOVAs with repeated measures, contrasting metrics as a function of the two releases and three sampling periods in each year. In order to meet assumptions of normality and homogeneity of variance we square-root transformed $((\sqrt{y}) + (\sqrt{y} + 1))$ proportional data and log transformed (log y + 1) all other data.

Drift response to changing flow

We sampled drift at fifteen different points in time during the 2010 releases, capturing periods of falling, rising, and relatively static, reference discharge. All samples were collected at site 5, near the gauging station, in riffle habitat (Table 1, Figs.

1, 4), because riffles yield higher BMI densities and are therefore most appropriate for drift sampling (Tonkin et al. 2009). We sampled drift using a 45 cm wide x 30 cm high Wildco drift net (0.363 mm mesh) with a General Oceanics rotary flowmeter (high-speed rotor) mounted in the aperture at 0.6 depth. The net was placed near the bank, because near-bank locations are most sensitive to changes in drift (Perry and Perry 1986). This sensitivity is a result of greater relative change in velocity near the bank and a propensity for higher drift densities near the bank (Perry and Perry 1986). The top of the net was emergent so that animals floating near the surface would be sampled. Set time was one hour; start and stop depth and temperature were recorded for each sample. Samples were preserved in the field and sorted and identified in the laboratory. We identified all aquatic and terrestrial taxa to family.

Poopenaut pond

We sampled the pond with a throw trap (cover photo) during April, May and July. Fauna was sampled with a throw trap using protocols derived from Sogard et al. (1987), Holmquist et al. (1989), Holmquist (1998), and Brostoff et al. (2010). Throw traps have been shown to be highly efficient, relative to other collecting devices, for quantitatively sampling benthic and demersal organisms in vegetated habitats (Kushlan 1981, Jacobsen and Kushlan 1987, Rozas and Minello 1997, Meyer et al. 2011). This method yields densities, because the trap encloses a known area, and virtually all fauna are removed. Processing time is longer than that required for other devices, but the size of the samples and quality of the data make this investment worthwhile (Meyer et al. 2011). The trap, constructed of sheet aluminum, was a 0.75 m x 0.75 m box without a top or bottom. The clearing device was a 0.75 m-wide framed and handled net (bar seine) with 0.5 mm square mesh. We threw the trap downwind (cover photo) at each randomly selected location in the pond and then pressed the bottom of the trap into the sediment. The bar seine was passed repeatedly through the trap ten times and was washed free of animals and detritus in a partially filled 0.75 m x 0.5 m plastic container that we floated in the pond. One person did all of the passes to insure consistency. In cases in which the water depth was greater than the height of the trap, a mesh cover was employed between passes. We transported the trap into and out of the valley on a pair of aluminum poles with a resulting palanquin-like arrangement.

We collected vegetation and physical data in conjunction with each trap sample. Before the disturbance associated with the bar seine passes, we estimated percent cover of bare substrate, litter, and green and senescent vegetation. We also recorded dominant vegetation, water temperature, and two measurements each for water depth, canopy height, and litter depth. We measured percent tree canopy cover, pH, total dissolved solids, and conductivity as described above for river work.

Samples were preserved in the field in 3 l containers and sorted and identified in the laboratory. We identified taxa to the lowest practical taxonomic level, most frequently to genus, but species identifications were made as well.

Categorical discharge and seasonal variables were the predictors for most of our drift and pond analyses. Effects of discharge on drift was assessed on two different scales: 1) planned comparisons as a function of hydrographic limb, regardless of change or lack thereof within a given net set, and 2) *post hoc* comparison of changes within individual net sets, regardless of timing relative to overall hydrographic limb.

Some factors for the latter set of comparisons had small sample sizes, precluding analysis via ANOVA. Examination of drift response at both scales is important, because initial responses to changing discharge may not be sustained through a given hydrographic limb (Perry and Perry 1986).

Most analysis of drift and pond results employed metrics and techniques that were similar to those outlined above. Drift density was determined using the standard of number of drift organisms per 100 m^3 (Allan 1995). Pond abundances are reported as per m^2 values, and pond richness and related metrics are scaled to 0.75 m^2. Large collections have more taxa than small collections, so we also assessed richness with expected number of species and families after scaling to the number of individuals in the sample with the fewest individuals (i.e., rarefaction; Hurlbert, 1971; Simberloff, 1972; Magurran 2004). Compensation for differing abundance also allowed comparison across drift samples, which necessarily had different total volumes. Rarefaction was based on minimum number of individuals/sample of 70 and 265, respectively, for drift and pond samples. Expected number of species and families for the two studies were thus $E(S_{70})$, $E(F_{70})$, $E(S_{265})$, and $E(F_{265})$. We used probability of interspecific encounter as a measure of evenness at the species level (PIE; Hurlbert, 1971). We calculated E(S), E(F), and PIE using the application Diversity. Results were assessed with ANOVAs, sign tests, and multiple, one- or two-tailed, independent t-tests.

Results

Assemblage Structure

Even the most consistent physical parameters varied by about a factor of two over the course of the sampling year. Depth varied from 24.8 to 59.0cm (mean= 38.0cm, Table 2), temperature ranged from 4.5 to 10.5°C (mean= 7.20 °C), and flow ranged from 30.7 to 66.8cm/sec. Other metrics were somewhat more variable (Table 2).

Habitat condition had mean scores that fell in the Optimal range for eight of the ten parameters (Table 3). Velocity/Depth Regime fell in the Marginal range because of the frequent lack of diverse flow regimes, and Frequency of Riffles was Suboptimal due to low occurrence of riffles. Although Epifaunal Substrate/Available Cover and Sediment Deposition fell in the Optimal range, these two parameters were close to Suboptimal because of lack of woody debris and sediment deposition, the latter primarily in pools. The overall score was Optimal (mean= 155; SE= 5.13).

The study collected 69 taxa representing 25 families and eight orders. There was a moderate level of evenness at the order level, although Ephemeroptera and Diptera made up the majority of the assemblage (Figs. 6, 7). There was more evenness at the family level (Figs. 8, 9) than at the order level, and the distribution lies between the log normal and MacArthur's broken stick models. Mean family richness was $16.3/2m^2$, which was reduced to D_{Mg}=2.70 after applying Margalef's correction for abundance, and family level dominance was 39.7% (Table 4). Species level rank-abundance showed a similar distribution (Figs. 10, 11) to family rank-abundance. There

Table 2. Means and standard errors for physical parameters (2007)

Metric	Mean	SE
Water depth (cm)	38.0	4.01
Water temperature (°C)	7.20	0.671
Flow (cm/sec)	50.7	5.16
Stream width (m)	22.7	4.54
Width (m):Depth (m) ratio	61.5	10.3
High water mark (m)	2.40	0.600
Percent shade	27.0	15.0
Percent cobble/boulder	58.0	11.9
Percent gravel	21.0	6.40
Percent sand	13.0	3.74
Percent silt	8.00	5.83

Table 3. Habitat characteristics from EPA Habitat Assessment Field Data Sheets with EPA condition categories. Each parameter is scored from 1-20; parameters 8-10 are scored from 1-10 for each bank and combined for the total score for the parameter in question. The overall score for a site is the sum of all ten parameters, with a maximum score of 200. SE= standard error. (Continued next page).

Habitat Parameter	Mean	SE	Condition Category
1. Epifaunal Substrate/ Available Cover	15.4	0.571	**Optimal** Greater than 70% of substrate favorable for epifaunal colonization and fish cover.
2. Embeddedness	16.3	0.808	**Optimal** Gravel, cobble, and boulder particles are 0-25% surrounded by fine sediment. Layering of cobble provides diversity of niche space.
3. Velocity/ Depth Regime	7.14	0.459	**Marginal** Only 2 of the 4 habitat regimes present.
4. Sediment Deposition	15.6	1.49	**Optimal** Little or no enlargement of islands or point bars and less than 5% (<20% for low-gradient streams) of the bottom affected by sediment deposition.
5. Channel Flow Status	18.7	0.522	**Optimal** Water reaches base of both lower banks, and minimal amount of channel substrate is exposed
6. Channel Alteration	18.4	0.481	**Optimal** Channelization or dredging absent or minimal; stream with normal pattern.
7. Frequency of Riffles	10.1	1.62	**Suboptimal** Occurrence of riffles infrequent; distance between riffles divided by the width of the stream is between 7 to 15.

Table 3 (cont.).
Habitat characteristics.

8. Bank Stability (Left)	8.71	0.360	**Optimal** Banks stable; evidence of erosion or bank failure absent or minimal; little potential for future problems. <5% of bank affected.
(Right)	9.14	0.404	
9. Vegetative Protection			**Optimal** More than 90% of the streambank surfaces and immediate riparian zone covered by native vegetation, including trees, understory shrubs, or nonwoody macrophytes; vegetative disruption through grazing or mowing minimal or not evident; almost all plants allowed to grow naturally.
(Left)	8.43	0.429	
(Right)	8.71	0.421	
10. Riparian Vegetative			**Optimal** Width of riparian zone >18 meters; human activities (i.e., parking lots, roadbeds, clear-cuts, lawns, or crops) have not impacted zone.
Zone Width (Left)	9.00	0.309	
(Right)	9.14	0.340	
Overall	**155**	**5.13**	**Optimal**

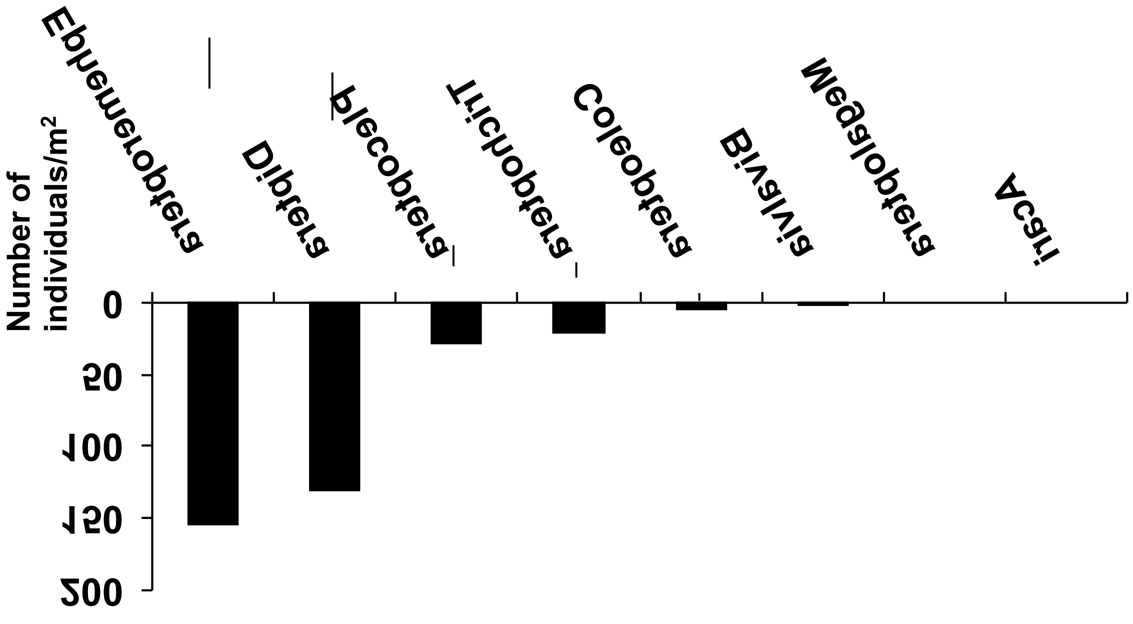

Fig. 6. Rank-abundance by order, plus Class Bivalvia (linear scale).

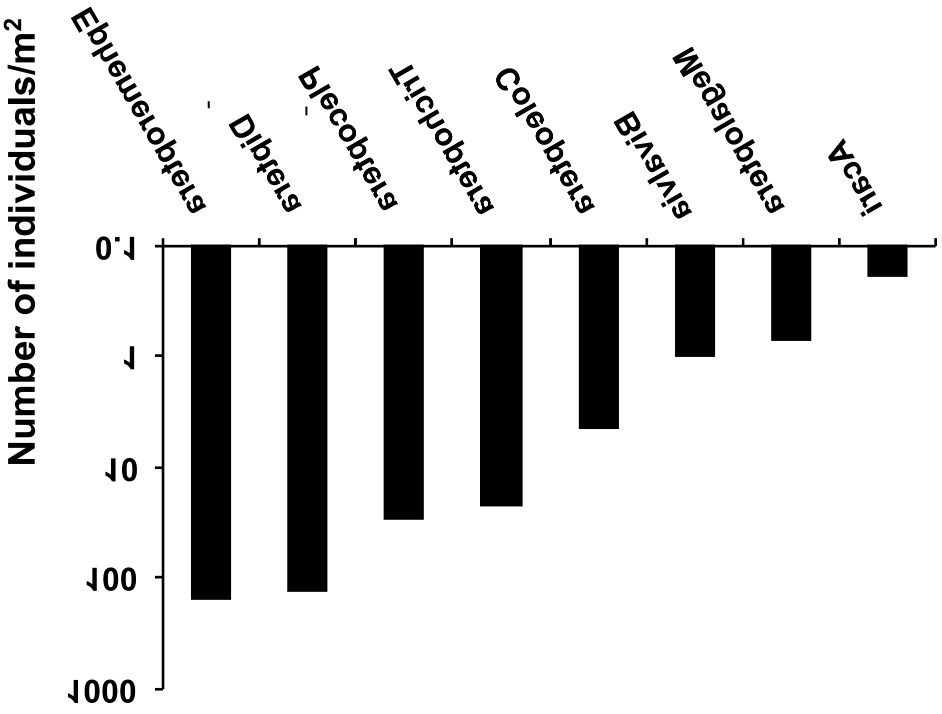

Fig. 7. Rank-abundance by order, plus Class Bivalvia (log scale).

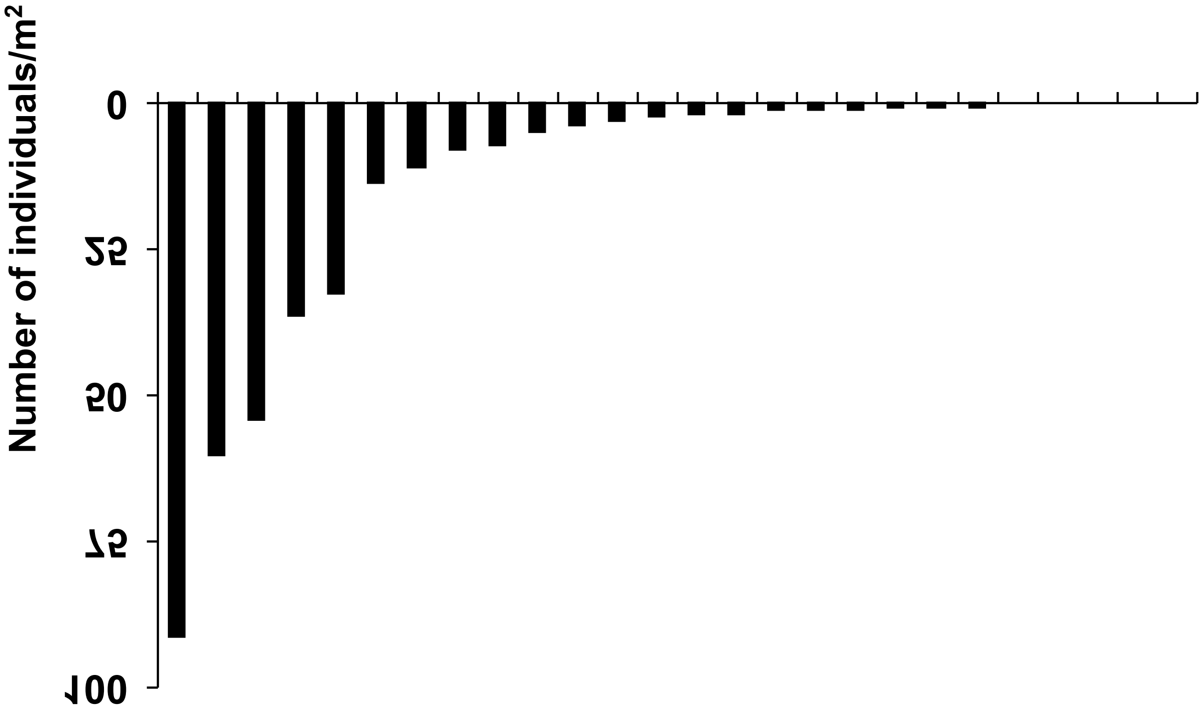

Fig 8. Rank-abundance by family sequence (linear scale). Shape of these curves, versus specifics for individual families, is the most important aspect of these graphs.

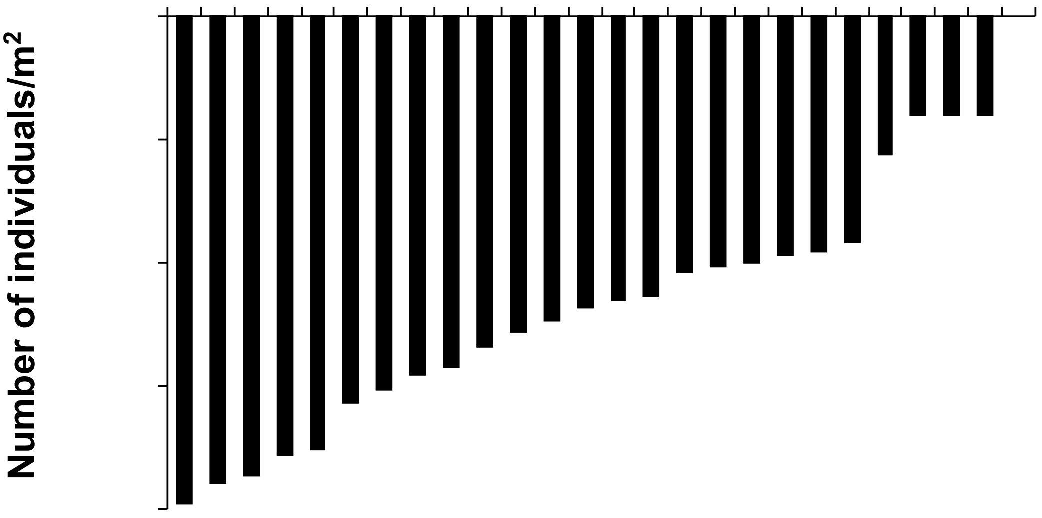

Fig. 9. Rank-abundance by family sequence (log scale).

Table 4. Means and standard errors for diversity metrics (2007-8).

	Mean	**SE**
Family Richness	16.3	0.365
Margalef's Corrected Family Richness	2.70	0.178
Percent Family Dominance	39.7%	4.11
Species Richness	41.7	3.40
Margalef's Corrected Species Richness	7.04	0.365
Percent Species Dominance	21.4%	5.30

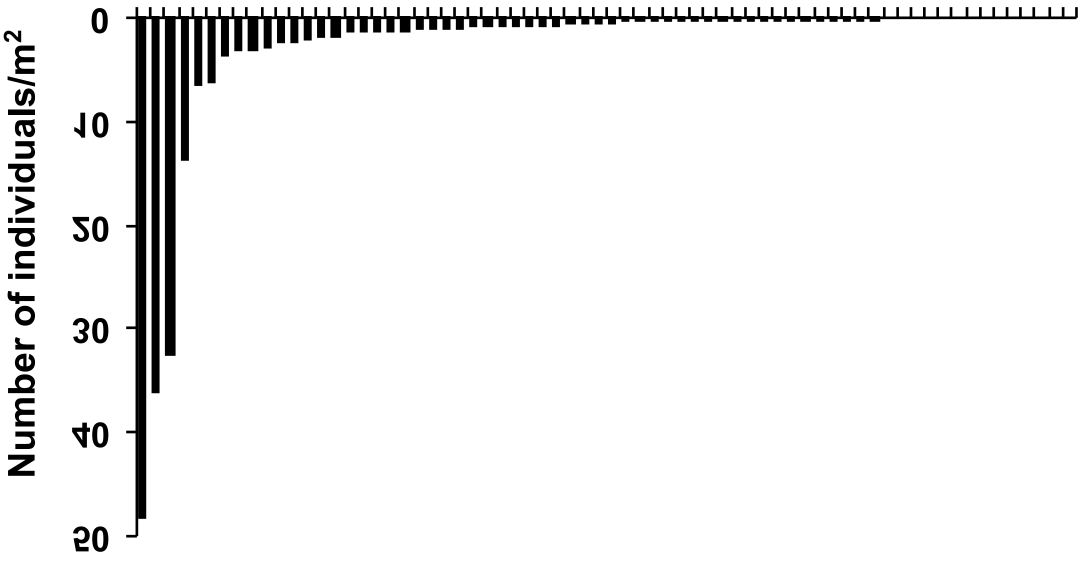

Fig 10. Rank-abundance at the species level (linear scale).

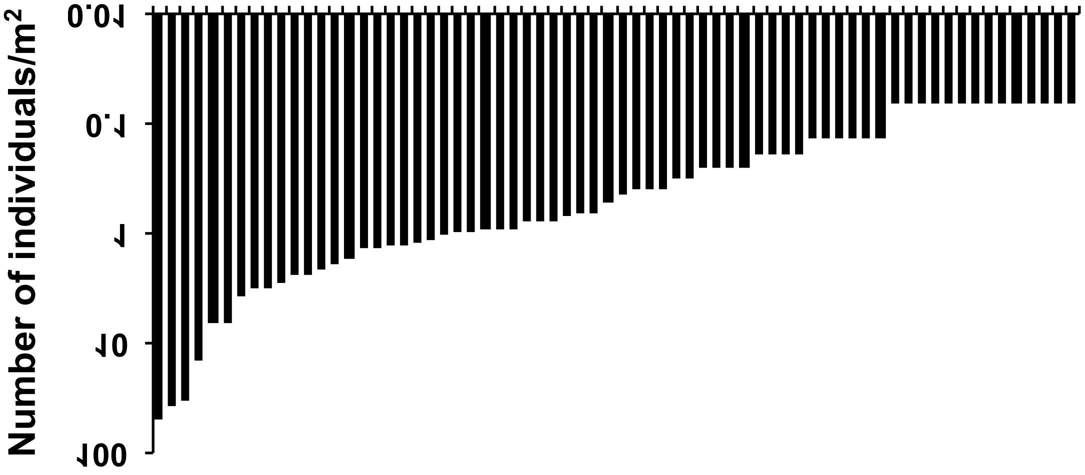

Fig 11. Rank-abundance at the species level (log scale).

was an average of 41.7 species per 2m^2, which converted to 7.04 after Margalef's correction, and species dominance was 21.4% (Table 4).

Ephemeroptera were found in every sample, and this order was dominated by Baetidae, Ephemerellidae, and Leptophlebiidae (mean individuals/m^2= 60.3, 54.1, and 32.5, respectively; Table 5). The only family collected in the study with a higher abundance was Chironomidae. All families had a high frequency of occurrence; the three previously noted families occurred in each sample and the remaining two families, Ameletidae and Heptageniidae, had frequencies of 0.750 and 0.875. Ephemerellidae was particularly speciose with nine taxa represented. The most abundant mayflies at the genus/species level were *Baetis* spp., *Ephemerella excrucians*, and *Paraleptophlebia* sp. (60.3, 48.3, and 32.5 individuals/m^2; Table 5). *Baetis* and *Paraleptophlebia* were found in every sample.

Plecoptera were lower in abundance (individuals/m^2= 28.3) but were still found in every sample (Table 5). There was a relatively high level of evenness among the stonefly families: Nemouridae, Perlidae, Chloroperlidae, and Perlodidae had 10.8, 8.38, 7.31, and 1.88 individuals/m^2, respectively. Only Chloroperlidae was represented in every sample. The most abundant species were *Hesperoperla pacifica and Malenka* sp. (6.38 and 6.31 individuals/m^2, respectively), and *Hesperoperla pacifica, Claassenia sabulosa,* and *Suwallia* sp. A had the highest frequency of occurrence at 0.625 (Table 5).

Trichoptera were similar to Plecoptera in abundance, and the most common caddisfly families were Hydropsychidae, Hydroptilidae, and Philopotamidae (13.6, 4.50, and 1.19 individuals/m^2, respectively; Table 5). Hydropsychidae and Hydroptilidae had

Table 5. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1° and 2° FFG), and California Tolerance Values (CTV) for 2007-9 assemblage characterization. Ephemeroptera and Plecoptera were all nymphs; Megaloptera, Trichoptera, and Diptera were larvae except for occasional pupae (pu); Coleoptera were either larvae (l) or adults (a); and Acari and Bivalvia were adults. FFGs: p= predator, cg= collector-gatherer, cf= collector-filterer, ph= piercer-herbivore, sc= scraper, sh= shredder. Tolerance values represent a general spectrum of tolerance to poor water quality, scored from 0 (highly intolerant) to 10 (highly tolerant). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Ephemeroptera	153	32.1	1.00			
Ameletidae	3.00	1.20	0.750			
Ameletus sp.	3.00	1.20	0.750	sc	cg	0
Baetidae	60.3	21.4	1.00			
Baetis spp.	59.0	21.3	1.00	cg	sc	4
Unknown	1.31	1.06	0.250	cg	sc	4
Heptageniidae	3.56	1.24	0.875			
Cinygmula sp.	0.625	0.246	0.625	sc	cg	4
Epeorus longimanus	0.625	0.498	0.250	sc	cg	4
Ironodes sp.	1.44	0.759	0.500	sc	cg	4
Rithrogena sp.	0.875	0.875	0.125	sc	cg	0

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Ephemeroptera, cont.						
Ephemerellidae	54.1	23.4	1.00			
Caudatella heterocaudata	0.0625	0.0625	0.125	cg	sc	1
Caudatella hystrix	1.31	0.744	0.500	cg	sc	1
Drunella grandis ingens	0.0625	0.0625	0.125	cg	sc	0
Ephemerella excrucians	48.3	22.8	0.875	cg	sc	1
Ephemerella dorothea infrequens	1.13	0.760	0.250	sh	cg	1
Ephemerella sp. A	0.250	0.250	0.125	cg	sc	1
Ephemerella sp. B	0.0625	0.0625	0.125	cg	sc	1
Ephemerella sp. C	0.188	0.188	0.125	cg	sc	1
Serratella teresa	2.81	2.08	0.375	cg		2
Leptophlebiidae	32.5	10.3	1.00			
Paraleptophlebia sp. A	32.5	10.3	1.00	cg	sh	4
Plecoptera	28.3	8.34	1.00			
Nemouridae	10.8	4.72	0.625			
Malenka sp.	6.31	3.80	0.500	sh		2
Podmosta delicatula	2.38	2.38	0.125	sh		2
Zapada cinctipes	1.69	1.69	0.125	sh		2
Unknown	0.375	0.375	0.125	sh	cg	2

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Plecoptera, cont.						
Perlidae	8.38	3.74	0.875			
Calineuria californica	1.81	0.647	0.625	p		3
Hesperoperla pacifica	6.38	3.74	0.625	p		2
Hesperoperla sp.	0.125	0.0818	0.250	p		2
Unknown	0.0625	0.0625	0.125	p		2
Perlodidae	1.88	0.976	0.500			
Cultus tostonus	0.0625	0.0625	0.125	p		2
Cultus sp.	0.313	0.313	0.125	p		2
Osobenus yakimae	0.938	0.938	0.125	p		2
Skwalla americana	0.125	0.125	0.125	p		2
Isoperla sp. A	0.250	0.250	0.125	p		2
Isoperla sp. B	0.188	0.188	0.125	p		2
Chloroperlidae	7.31	3.05	1.00			
Alloperla sp.	0.250	0.250	0.125	p		1
Haploperla chilnualna	1.13	0.603	0.625	p	cg	1
Plumiperla sp.	0.938	0.868	0.250	p		1
Suwallia sp. A	3.00	1.46	0.625	p		1
Suwallia sp. B	1.94	1.45	0.250	p		1
Unknown	0.0625	0.0625	0.125	p		1

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Megaloptera						
Corydalidae	0.688	0.298	0.500			
Orohermes crepusculus	0.688	0.298	0.500	p		0
Trichoptera	21.3	8.13	0.875			
Philopotamidae	1.19	0.886	0.250			
Dolophilodes sp.	1.19	0.886	0.250	cf		2
Polycentropodidae	0.875	0.337	0.500			
Polycentropus sp.	0.875	0.337	0.500	p	cf	6
Hydropsychidae	13.6	7.58	0.750			
Hydropsyche sp.	13.6	7.58	0.750	cf		4
Rhyacophilidae	0.375	0.375	0.125			
Rhyacophila sp. A	0.375	0.375	0.125	p		0
Hydroptilidae	4.50	2.02	0.750			
Hydroptila sp. A	3.88	1.77	0.500	ph	sc	6
Hydroptila sp. B	0.438	0.371	0.250	ph	sc	6
Hydroptila sp. (pu)	0.188	0.132	0.250	ph	sc	6
Lepidostomatidae	0.750	0.423	0.500			
Lepidostoma sp.	0.750	0.423	0.500	sh		1

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Coleoptera	4.38	2.27	0.625			
Hydrophilidae	0.0625	0.0625	0.125			
Enochrus sp. (a)	0.0625	0.0625	0.125	ph		5
Elmidae	4.31	2.28	0.625			
Cleptelmis addenda (l)	2.25	1.97	0.375	cg	sc	4
Cleptelmis addenda (a)	0.0625	0.0625	0.125	cg	sc	4
Heterlimnius sp. (l)	0.250	0.250	0.125	cg	sc	4
Optioservus quadrimaculatus (a)	1.25	0.366	0.625	cg		4
Rhizelmis nigra (l)	0.375	0.375	0.125	sc	cg	2
Zaitzevia sp. (a)	0.0625	0.0625	0.125	cg		4
Unknown (l)	0.0625	0.0625	0.125	cg		4
Diptera	132	29.0	1.00			
Chironomidae*	92.1	19.0	1.00	cg	p	6
Psychodidae	0.0625	0.0625	0.125			
Pericoma sp.	0.0625	0.0625	0.125	cg		4
Simuliidae	36.2	14.6	0.750			
Simulium spp.	36.1	14.5	0.750	cf		6
Simulium canadense (pu)	0.0625	0.0625	0.125	cf		6

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		**Frequency**	**1°FFG**	**2°FFG**	**CTV**
	Mean	SE				
Diptera, cont.						
Tipulidae	2.25	0.835	0.750			
Antocha sp.	0.125	0.0818	0.250	cg		3
Dicranota sp.	1.25	0.866	0.250	p		3
Hexatoma sp.	0.875	0.515	0.375	p		2
Empididae	1.06	0.427	0.500			
Clinocera sp.	0.188	0.188	0.125	p		6
Hemerodromia sp.	0.438	0.371	0.250	p		6
Wiedemannia sp.	0.0625	0.0625	0.125	p		6
Clinocera/Wiedemannia (pu)	0.188	0.188	0.125	p		6
Unknown Empididae A	0.0625	0.0625	0.125	p		6
Unknown Empididae B	0.125	0.125	0.125	p		6
Acari						
Hydrachnidae	0.125	0.125	0.125			
Hydrachna sp.	0.125	0.125	0.125	p		5
Hydryphantidae	0.0625	0.0625	0.125			
Thyadinae	0.0625	0.0625	0.125	p		5

Table 5, cont. Densities (per m^2; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1°, 2° FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance Mean	 SE	**Frequency**	**1°FFG**	**2°FFG**	**CTV**
Mollusca, Bivalvia						
Veneroida	0.875	0.806	0.250			
Sphaeriidae	0.875	0.806	0.250			
Sphaerium sp.	0.875	0.806	0.250	cg		8
Total Individuals	**341**	**45.0**				

* Individual chironomid morphospecies were separated and counted but most were not identified

the highest frequency of occurrence at 0.750. The most common taxa were *Hydropsyche* sp., *Hydroptila* sp. A, and *Dolophilodes* sp. (13.6. 3.88, 1.19 individuals/m^2, respectively; Table 5).

Coleoptera were relatively uncommon (4.38 individuals/m^2), and Elmidae (riffle beetles) and Hydrophilidae (water scavenger beetles) were the only families collected (4.31 and 0.0625 individuals/m^2, respectively; Table 5). Of the seven collected Coleoptera taxa, six were elmids, and both larval and adult elmids occurred in the samples. The elmids *Cleptelmis addenda* and *Optioservus quadrimaculatus* were the most abundant beetles (2.31 and 1.25 individuals/m^2, respectively); *Optioservus* had the highest frequency of occurrence (0.625). *Atractelmis wawona* (the Wawona riffle beetle), a federal species of concern, was not encountered.

Diptera was the most abundant order (132 individuals/m^2), and in turn Chironomidae (midges; 92.1 individuals/m^2) and Simuliidae (black flies; 36.2 individuals/m^2) were the most common dipterans (Table 5). Chironomidae was the only dipteran family found in each sample. Tipulidae (crane flies) and Empididae (dance flies) were also important both in terms of abundance and species richness (Table 5).

We also collected dobsonflies (Megaloptera), water mites, and clams, all in small numbers (Table 5). *Orohermes crepusculus*, the dobsonfly in our samples, was the largest animal that we collected; some specimens reached 4.5cm. No New Zealand mudsnails (*Potamopyrgus antipodarum*), or any other gastropods, were collected.

The sampled taxa represented a variety of feeding groups (Table 5). The majority of species were either predators (29) or collector-gatherers (20). There were fewer scrapers (6), shredders (6), collector-filterers (4), and piercer-herbivores (4), although scraping was frequently a secondary functional feeding mode. Important predator groups included stoneflies, crane flies, dance flies, and mites. Ephemerellid mayflies and riffle beetles were generally collector-gatherers. Most of the primary scrapers were heptageniid mayflies, most of the shredders were nemourid stoneflies, most of the piercer-herbivores were hydroptilid caddisflies, and the only collector-filterers were black flies and some of the caddisflies.

The proportional importance of the various functional feeding groups shifted significantly when considered as proportion of individuals (Table 6) instead of relative to numbers of taxa. Collector-gatherers accounted for 70.9% of total individuals-- a function of several abundant mayfly species (Table 5). Although predators accounted for a majority of taxa, due in large part to the speciose stoneflies (Table 5), predators only represented 7.47% of individuals (Table 6). In contrast, the four collector filterer taxa represented 13.5% of total individuals (Table 6), a function of abundant black flies (Table 5). Percent scrapers was notably low at only 1.98% (Table 6).

Tolerance values ranged from 0 to 8, but there were far more intolerant taxa (tolerance from 0 to 3; 36 taxa) than intolerant taxa (tolerance from 8 to 10; one taxon, the clam *Sphaerium* at a value of 8; Table 5). This one tolerant taxon represented 1.4% of taxa and only 0.26% of individuals. Tolerance values for mayflies and stoneflies were low, ranging from 0 to 4 and 1 to 3, respectively. Our one megalopteran species had a tolerance of 0. The caddisflies, beetles, and flies ranged higher (0 to 6, 2 to 5, and 2 to 6, respectively; Table 5). The unweighted mean tolerance by taxon was 3.1. Hilsenhoff's biotic index, which effectively weights tolerance by abundance of individual

Table 6. Mean percentage of fauna (by individuals) and standard errors for primary functional feeding groups from 2007-8 assemblage characterization.

	Mean	**SE**
Percent Scrapers	1.98	0.532
Percent Predators	7.47	1.76
Percent Collector-Gatherers	70.9	5.35
Percent Shredders	4.30	1.61
Percent Collector-Filterers	13.5	4.94
Percent Piercer-Herbivores	1.80	0.796

taxa, was 4.01 (SE= 0.338). Another measure of river health, Percent Ephemeroptera-Plecoptera-Trichoptera (EPT), was relatively high at 78.8% of total individuals (SE= 5.04), and 64% of taxa.

Initial data exploration via multiple regression yielded few significant models. Positive predictors included flow for simuliids (black flies), vegetation in the riparian zone (Table 3) for chironomids (midges), and lack of sediment deposition (Table 3) for baetid mayflies.

Some seasonal trends were apparent, particularly when spring-summer and fall-winter months were compared (Table 7). Diptera increased three-fold during the fall and winter (from a mean of 66.9 to 196 individuals/m^2; Table 7). Much of this increase was driven by an increase in simuliid black flies from zero to a mean of 71.8 individuals/m^2 (Table 7, Fig. 12). Chironomid midges, particularly Tanytarsini, also

Table 7. Mean values (SE= standard error) for selected metrics as a function of period during which sampling occurred: Spring-Summer (March through August 07) or Fall-Winter (September 07 through February 08). Most response variables were tested for seasonal differences and the majority were non-significant; only significant results are presented here. P-values are the result of two-tailed Mann-Whitney U tests. *Simulium* is a black fly (Diptera: Simuliidae); *Serratella* is a mayfly (Ephemeroptera; Ephemerellidae); %CF= Percent Collector-Filterers; %EPT= Percent Ephemeroptera-Plecoptera-Trichoptera; %Dominance (Sp)= Percent dominance by the most common species in each sample; HBI= Hilsenhoff's Biotic Index (larger values indicate increased tolerance to poor water quality).

	Spring-Summer		**Fall-Winter**		
	Mean	**SE**	**Mean**	**SE**	**p**
Diptera	66.9	27.9	196	18.6	0.0209
Simulium sp.	0.500	0.354	71.8	11.9	0.0202
Serratella teresa	5.63	3.86	0.00	0.00	0.0472
%CF	2.75	1.78	24.3	5.79	0.0209
%EPT	78.7	5.04	44.8	0.818	0.0209
%Dominance (Sp)	29.9	9.04	12.9	0.890	0.0209
HBI	3.28	0.350	4.75	0.226	0.0209

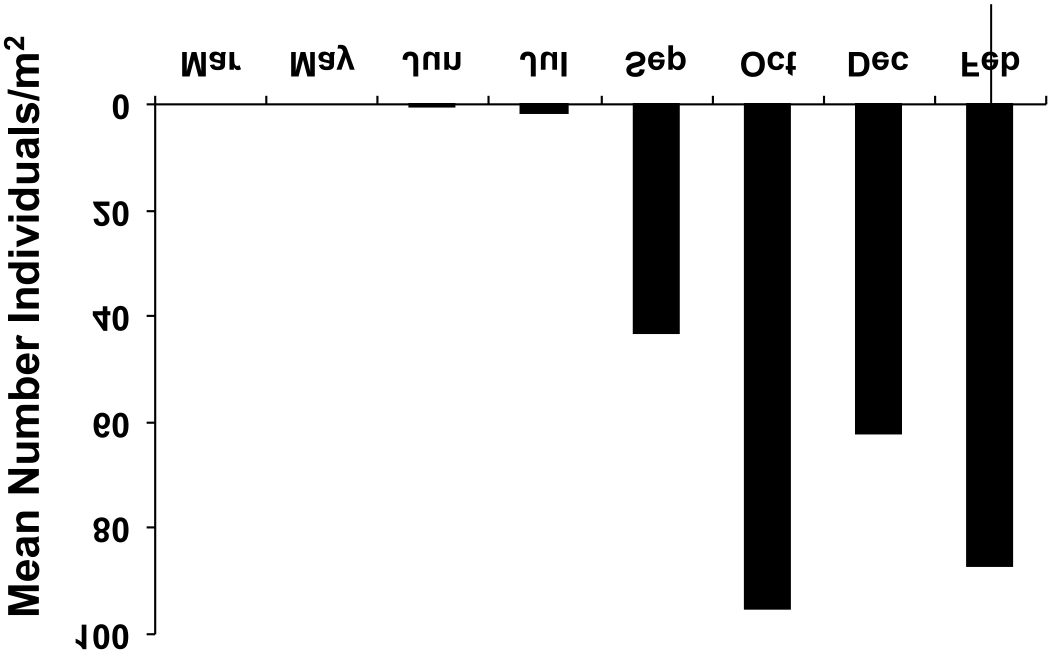

Fig. 12. *Simulium* (black flies; Diptera: Simuliidae) densities during study year.

increased from a spring-summer mean of 63.0 to a fall-winter mean of 121 individuals/m^2 (27.4 and 19.3 SE, respectively), although these differences were not significant (Mann-Whitney U test, p= 0.0814). These increases in dipteran abundance were combined with a decrease in number of %Ephemeroptera-Plecoptera-Trichoptera from a mean of 228 to 177 individuals/m^2, e.g., *Serratella teresa* (Table 7). In turn, %EPT decreased (from over 80% to 30%; Table 7, Fig. 13), and %Collector-Filterers, the simuliid functional feeding group, increased (from zero to above 20%; Table 7, Fig. 14). The dominant functional feeding group, collector-gatherers, decreased from 91% to about 60% during this time (Fig. 14), though this was not a significant change (Mann-Whitney U test, p= 0.149). Most dipterans collected in the study had higher tolerance values than the rest of the taxa (Table 5), and Hilsenhoff's Biotic Index increased steadily from 2.29 to ~5.0 from spring to winter (Fig. 15, Table 7). Percent Species Dominance, however, decreased from 56% to ~15% during this time period (Fig. 16, Table 7), whereas % Family Dominance did not show as steady a decline (Fig. 16).

Large rock substrata (boulders and submerged slabs) yielded higher means (mean= 767 individuals/m^2, SE= 719) than cobble substrata, but variability was very high, as some samples had almost no fauna present. Ephemeroptera were abundant in one sample but absent in the others (mean= 294 individuals/m^2, SE= 294). Adult and larval elmid (riffle) beetles were common in the same abundant sample and again absent in the other rock scrapings (mean= 276 individuals/m^2; SE= 276). Diptera were also present in large numbers (mean= 104 individuals/m^2, SE= 68.2). Trichoptera and Plecoptera were less abundant (~50 individuals/m^2 each).

Fig. 13. Percent Ephemeroptera-Plecoptera-Trichoptera during study year.

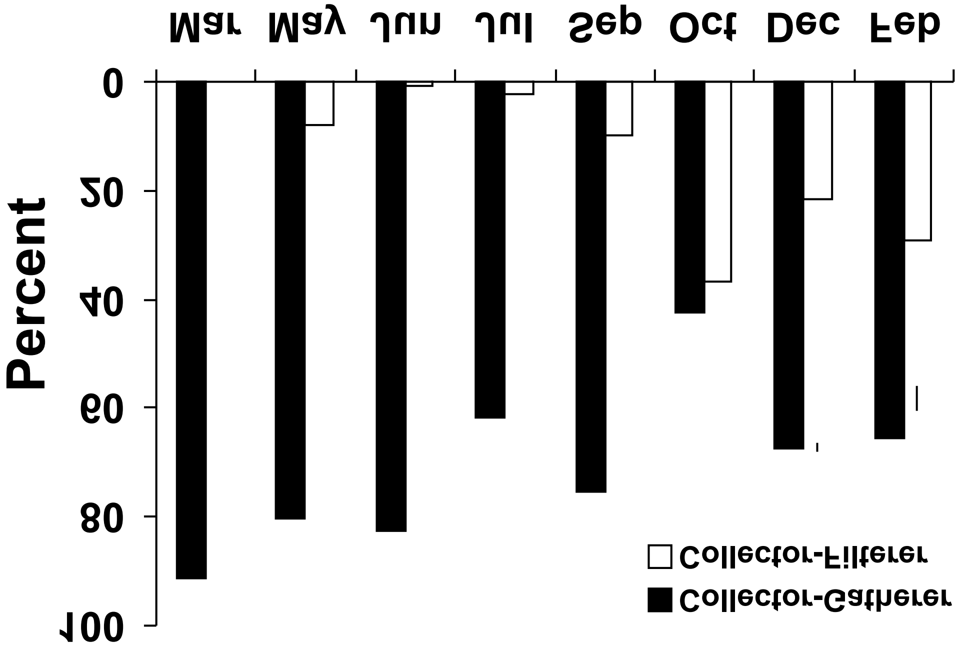

Fig.14. Percent Collector-Gatherers and Collector-Filterers during study year.

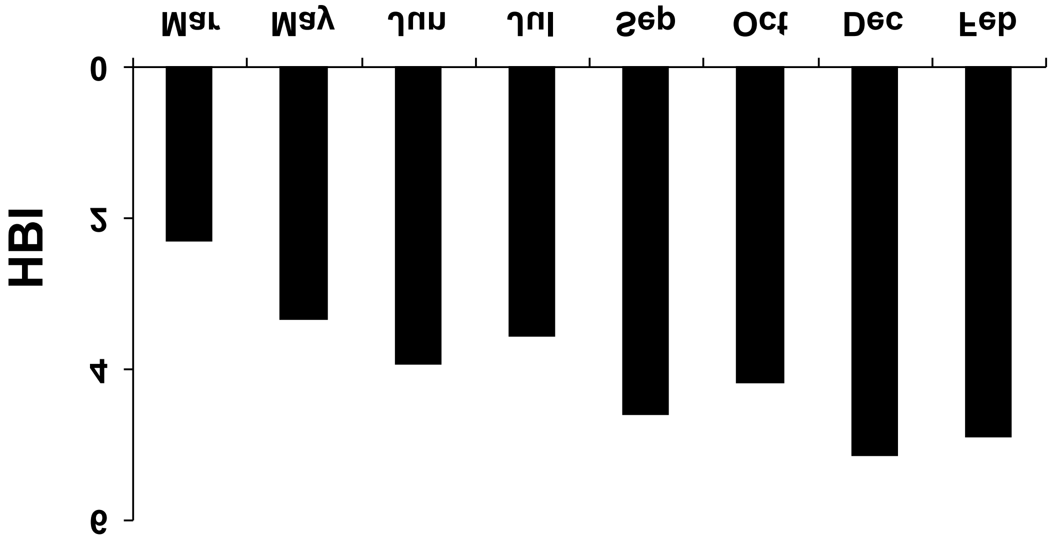

Fig. 15. Hilsenhoff Biotic Index during study year.

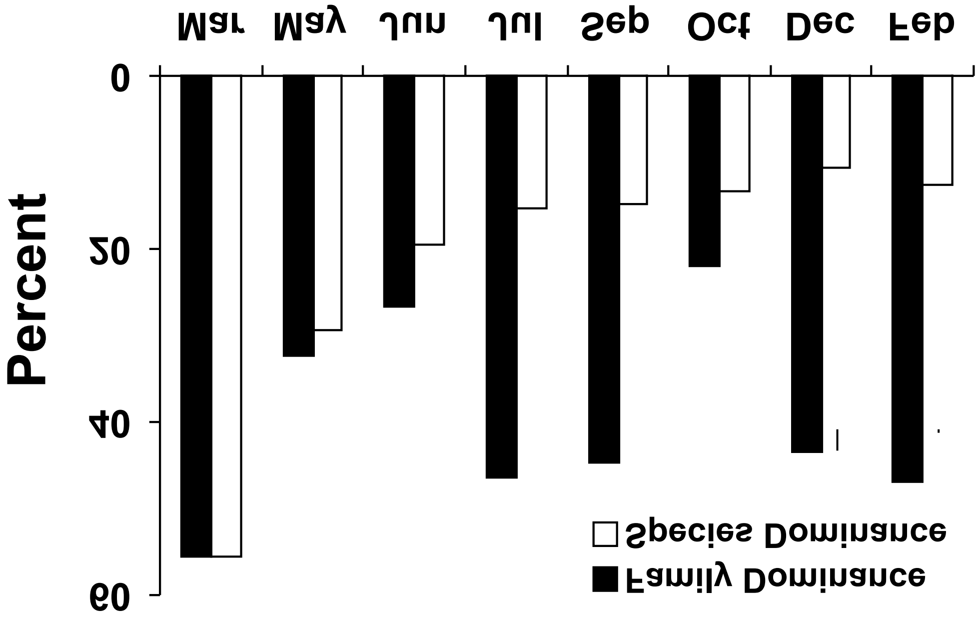

Fig. 16. Percent Family and Species Dominance during study year.

Response to Experimental Releases

Habitat variables recorded in association with the 2008 and 2009 releases were generally similar to those recorded during 2007-8 baseline data acquisition. Water depth (37.5 cm, SE= 3.10) and water temperature (mean= 7.00 °C, SE= 0.289) in summer 2008 were almost identical to baseline 2007-8 values (Table 2), whereas flow (mean= 57.0 cm/sec, SE= 5.28), stream width (mean= 25.6 m, SE= 2.06), and width:depth ratio (mean= 75.9, SE= 6.82) were somewhat higher during our release-associated sampling during summer of 2008. Mean water depth, water temperature, and flow were higher in summer 2009 than in summer 2008 (2009 means: 40.6 cm, SE= 2.13; 10.8 °C, SE= 0.56; 60.1 cm/sec, SE= 6.1, respectively). Mean conductivity, pH, and total dissolved solids were 10.1 μS/cm (SE= 0.38), 7.0 (SE= 0.020), and 4.9 ppm (SE= 0.20), respectively, for the summers of 2008 and 2009 combined; differences between years were minimal. Tree cover averaged only 5.1% (SE= 0.98). Mean algal dry mass was 5.12 gdm/m^2 (SE= 0.979).

In 2008, we collected 9,659 individual arthropods from 60 taxa representing 28 families and nine orders. Twenty-eight taxa collected in the 2007-8 baseline sampling were absent, but eighteen taxa that were absent that year were catalogued during the summer 2008 experiment. There was more total abundance in 2009: 13,547 individuals. There were, however, only 51 taxa collected in 2009; 71 different taxa were collected over both years. Total family richness in 2009 (29) was similar to that of 2008, as was order richness (9). We collected thirty-two families and ten orders across both years.

There were changes in the invertebrate assemblages that occurred in concert with the experimental releases, but these effects differed between 2008 and 2009 (Figs. 17-20). The 2008 release changed an assemblage with relatively high dominance, apparent in the log normal distribution in the family and species rank-abundance plots before the event (Figs. 17, 18), to an assemblage with greater evenness, apparent in the broken stick distribution immediately after the release (Figs. 17, 18). Two months after the release, the family rank-abundance relationship was similar to that from before the event (Fig. 17), and the species rank-abundance plot showed less evenness still (Fig. 18). Immediately after the 2009 release, family and species evenness was lower than before the release and lower still two months later, with three families demonstrating strong dominance (Figs. 19, 20).

Most assemblage-level metrics showed strong responses to the release (Table 8). Overall abundance fell in association with the releases and then rebounded. Overall abundances were higher in 2009 than in 2008. Family richness decreased in association with the releases, although after correcting for differing abundances (Margalef's correction) family richness increased after the 2008 release (Table 8). Margalef's family richness was higher in 2008 than in 2009. Species richness, with and without Margalef's correction, fell following the release and did not return to pre-release richness after two months. Margalef's species richness was also higher in 2008. Family dominance fell in response to the release and was still lower than pre-release levels after two months in 2008, whereas the opposite pattern obtained in 2009 (Table 8). Percent Ephemeroptera-Plecoptera-Trichoptera (%EPT) also showed opposing trends, increasing following the 08 release and decreasing after the 09 release (Table

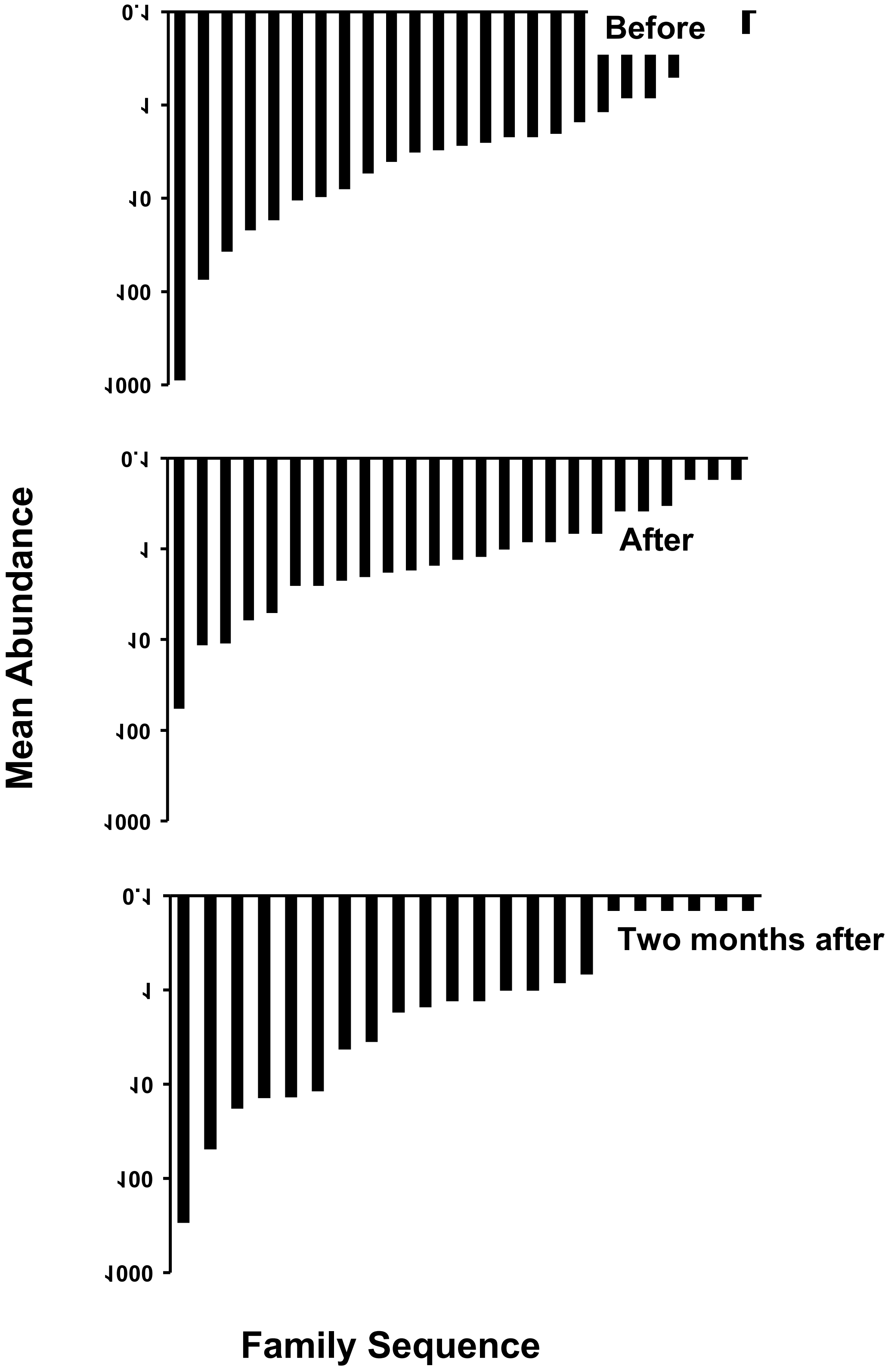

Fig. 17. Rank-abundance by 2008 sampling event at the family level (log scale).

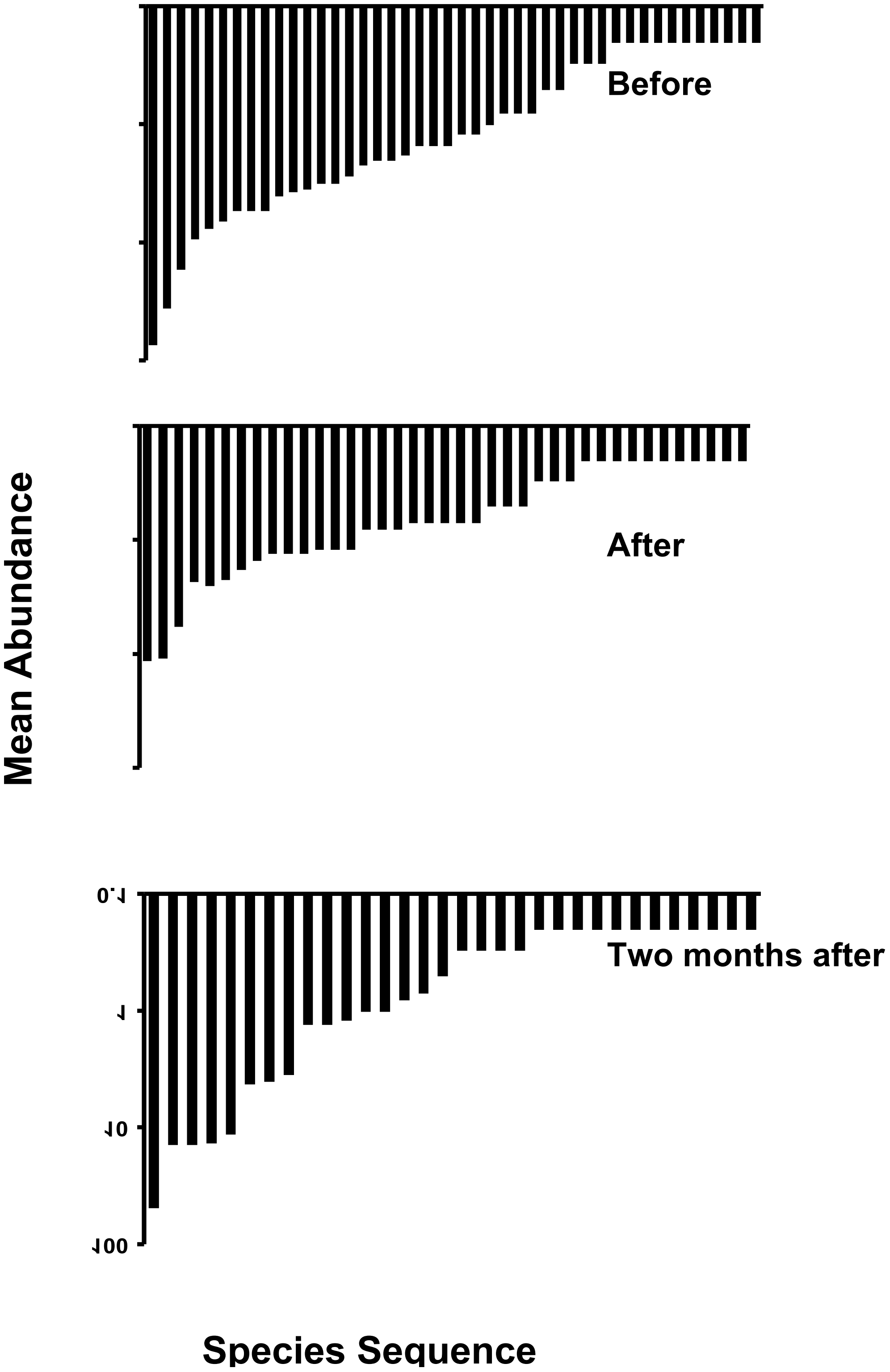

Fig. 18. Rank-abundance by 2008 sampling event at the species level (log scale).

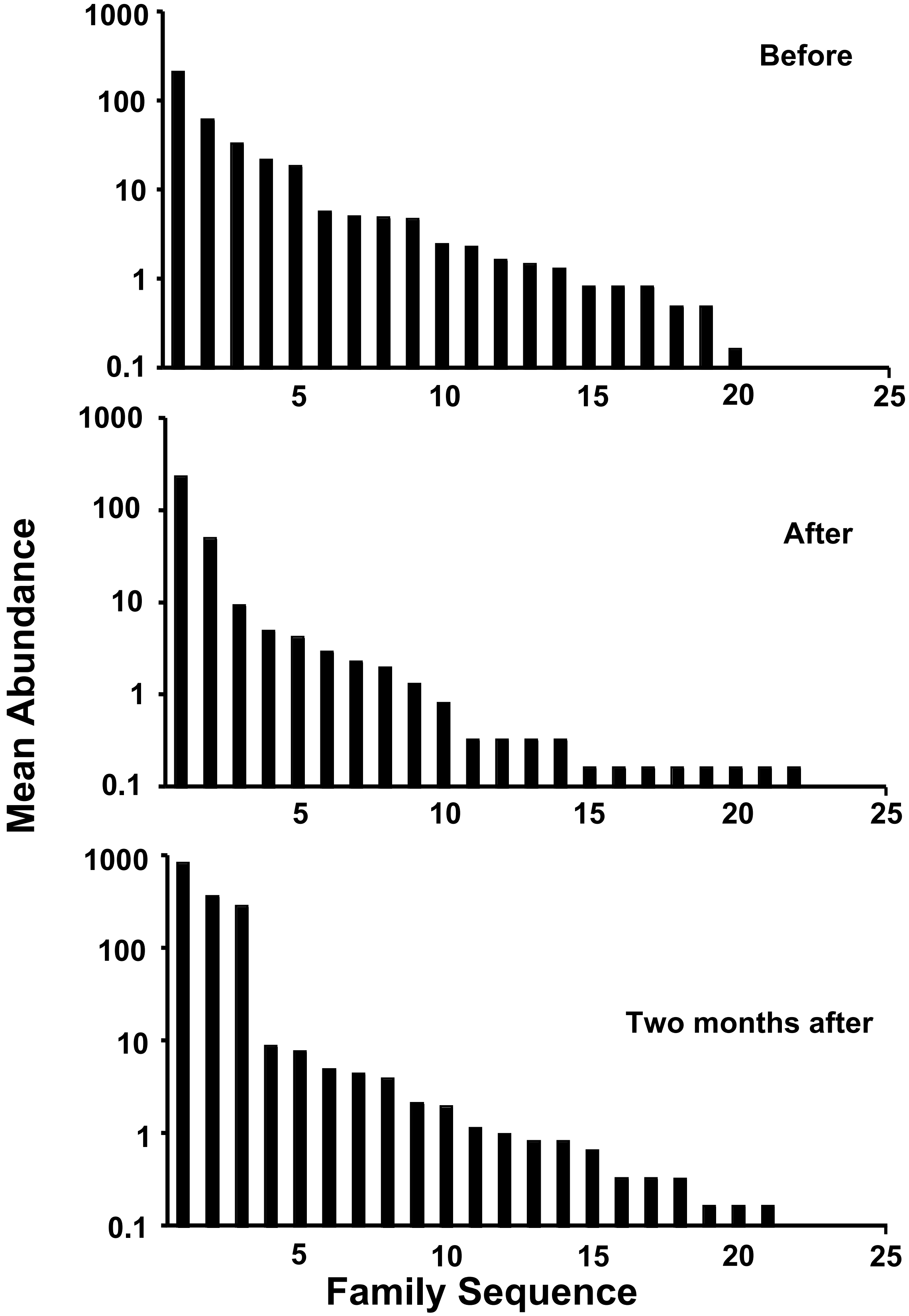

Fig. 19. Rank-abundance by 2009 sampling event at the family level (log scale).

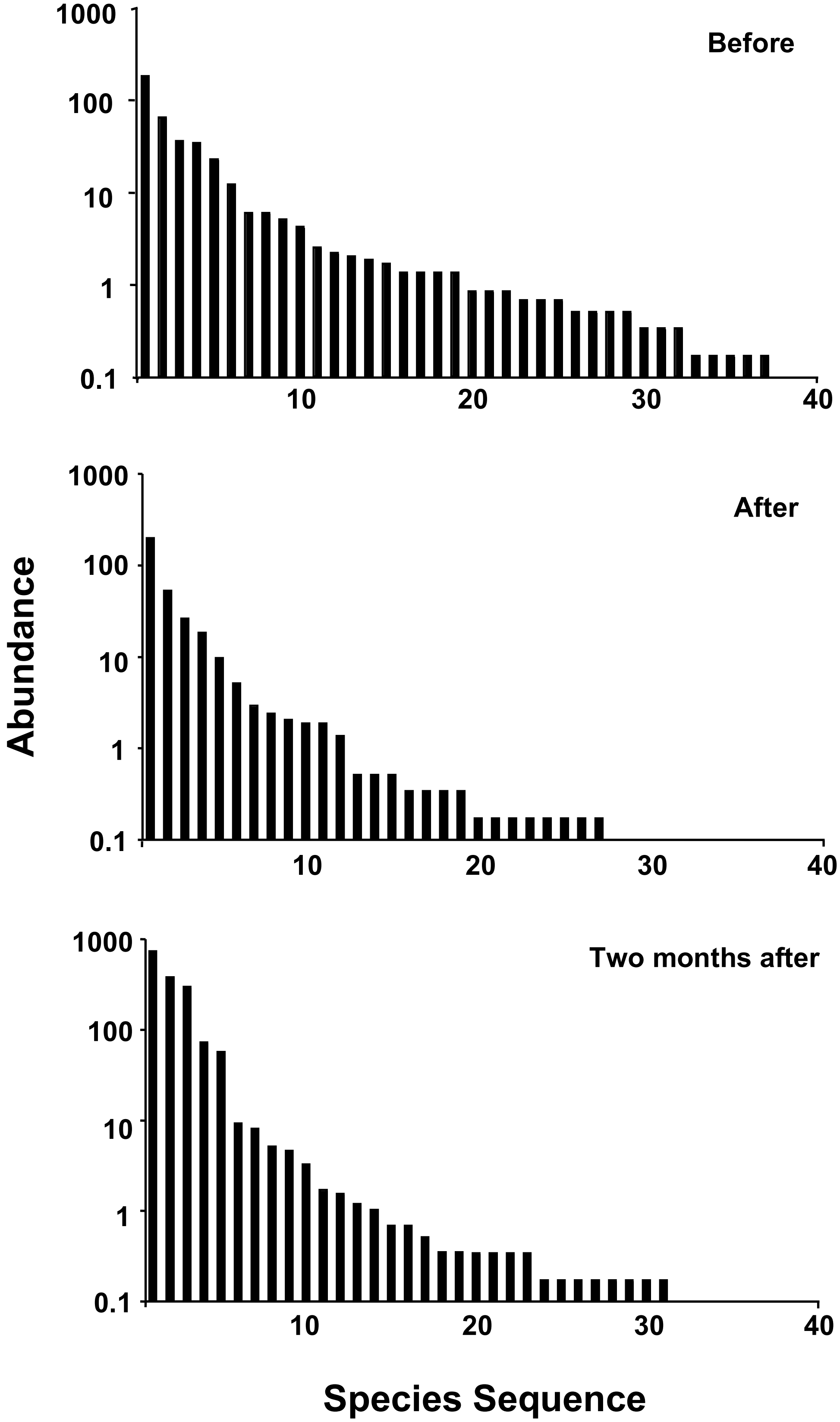

Fig. 20. Rank-abundance by 2009 sampling event at the species level (log scale).

Table 8. Response of mean (SE) macroinvertebrate assemblage-level variables and algal biomass to the 2008 and 2009 experimental release (all per-square-meter). %EPT= percent Ephemeroptera + Plecoptera + Trichoptera. "Sampling" references differences among the Before, After, and Two months after sampling periods. * represents p< 0.05; ** represents p< 0.01.

		Before		**After**		**2 mo after**		**ANOVA**		
	Year	x	SE	x	SE	x	SE	**Sampling**	**Year**	**Sampling * Year**
Total Individuals	08	1086	287	112	34	415	123	<0.0001**	0.0081**	0.0060**
	09	390	89.5	321	54.9	1547	231			
Family Richness	08	16.3	0.494	13.2	1.68	12.7	1.33	0.00081**	0.096	0.099
	09	12.8	1.42	8.83	0.980	11.5	0.922			
Margalef's Corrected Family Richness	08	2.25	0.0584	2.74	0.169	2.051	0.269	0.0037**	0.0067**	0.00038**
	09	2.01	0.183	1.37	0.158	1.44	0.109			
Species Richness	08	42.8	2.48	22.7	3.22	29.0	3.11	<0.0001**	0.052	0.11
	09	27.3	3.55	19.2	1.49	23.2	1.96			
Margalef's Corrected Species Richness	08	6.13	0.258	4.83	0.316	4.86	0.483	<0.0001**	0.0023**	0.70
	09	4.46	0.476	3.18	0.199	3.02	0.213			
% Family Dominance	08	77.6	3.61	47.8	5.51	61.1	8.00	0.34	0.82	0.0082**
	09	58.3	5.78	70.5	6.97	62.2	8.42			
% EPT	08	20.5	3.35	44.3	5.52	32.7	6.72	0.30	0.61	0.0038**
	09	39.3	6.55	26.8	6.72	22.4	4.86			
Hilsenhoff's Biotic index	08	5.47	0.0876	4.97	0.287	5.49	0.149	0.058	0.40	0.014*
	09	5.10	0.239	5.56	0.105	5.77	0.050			
Algal Biomass (gdm)	08	9.00	1.99	1.91	0.590	4.46	0.561	0.00077**	0.34	0.0027**
	09	3.79	0.395	3.83	1.020	2.93	0.760			

8). Hilsenhoff's Biotic Index also showed differing response as a function of year. The 2008 release caused a five-fold reduction in algal biomass, but there was about a 50% recovery in the two months that followed, whereas in 2009 there was little algal response (Table 6).

All orders decreased in abundance in association with the releases (Table 9), with the striking exception of Diptera in 2009. In contrast, Diptera in 2008 showed the greatest proportional and absolute release-induced losses, falling from a mean of 892 to 61 individuals per square meter—a 93% loss. Prior to the release, Diptera dominated the assemblage at 82%; after the release, Diptera was still the most abundant order, but this group represented only 54% of the total density. Less tolerant taxa lost density as well, but these losses were proportionally lower for Ephemeroptera, Plecoptera, and Trichoptera (Table 9). Less abundant taxa, such as Coleoptera, Acari, and Bivalvia all had reduced densities as well.

By two months after the releases, however, most taxa again increased in number, though most groups did not reach the densities seen before the release (Table 9). Ephemeroptera, Plecoptera, and Trichoptera had divergent recoveries in both 2008 and 2009. Ephemeroptera and Trichoptera recovered to a greater extent than Plecoptera, the former generally achieving abundances greater than before the releases. Ephemeroptera rebounded more strongly in 2009 than in 2008. Coleoptera had a similar response to Ephemeroptera, whereas Acari and Bivalvia showed no recovery, although both of these groups were relatively uncommon before the releases (Table 9). Following the two month recovery period, dipteran dominance was intact.

Table 9. Response of mean (SE) macroinvertebrate order densities per meter square to the 2008 and 2009 experimental release (all per-square-meter). %EPT= percent Ephemeroptera + Plecoptera + Trichoptera. "Sampling" references differences among the Before, After, and Two months after sampling periods. * represents $p< 0.05$; ** represents $p< 0.01$.

		Before		**After**		**2 mo after**		**ANOVA**		
	Year	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	**Sampling**	**Year**	**Sampling * Year**
Ephemeroptera	08	90.8	14.6	25.2	7.76	67.7	17.1	<0.0001**	0.017*	0.035*
	09	122	33.4	56.8	12.7	299	57.4			
Plecoptera	08	86.2	25.9	15.7	5.48	16.8	4.62	0.0029**	0.21	0.051
	09	27.2	15.0	12.5	4.19	12.0	3.42			
Trichoptera	08	10.0	2.31	8.00	2.35	18.2	5.96	0.029*	0.14	0.72
	09	9.83	5.45	4.50	1.98	12.5	2.45			
Coleoptera	08	2.83	1.014	0.833	0.401	2.17	0.703	0.19	0.46	0.67
	09	2.33	1.94	0.833	0.477	2.33	1.58			
Diptera	08	892	260	61.0	21.2	310	112	0.00018**	0.0095**	0.00031**
	09	228	51.4	246	56.4	1221	213			
Acari	08	2.17	1.078	0.833	0.477	0.167	0.167	0.091	0.015*	0.39
	09	0.333	0.333	0.000	0.000	0.000	0.000			
Veneroidea (Bivalvia)	08	2.00	1.18	0.833	0.833	0.667	0.422	0.14	0.25	0.98
	09	1.33	1.33	0.000	0.000	0.000	0.000			

Acari were more abundant in 2008, but the two most abundant orders, Diptera and Ephemeroptera, had their highest numbers in 2009.

Chironomid midges dominated the 2008 assemblage at the family level throughout all sampling periods despite the dramatic flood losses (Table 10). Nemourid stoneflies, particularly the genus *Malenka*, and baetid mayflies were also important in all phases of the study, although baetids became more dominant after the release and nemourids less so. Leptophlebiid mayflies ranked third, fourth, and third among families at the three different 2008 sampling events (Table 10). One species of *Paraleptophlebia* dominated the family before and after the release, but a congeneric species dominated after two months. Ephemerellid mayflies were speciose and initially ranked fourth in family abundance, but were ranked fifth after the release. Ephemerellids were almost absent two months after the 2008 experimental release and were represented entirely by *Serratella micheneri* (Table 10). Simuliid black flies were present in low numbers until two months after the release, at which time black flies reached 13.5 individuals per square meter and ranked fifth among all families.

A variety of other family-level responses to the 2008 release were observed. Twenty of the 28 families collected during the experiment were at their highest densities before the release (Table 10). Seven families were collected at their lowest densities after the release, but two families, Chloroperlidae (Plecoptera) and Lepidostomatidae (Trichoptera), were at their highest densities at this time. By two months after the 08 release, there were some notable increases and decreases. As indicated above, there were increases in baetids and simuliids, and polycentropodid and hydroptilid caddisflies were also at their highest levels at this time (Table 10). In contrast, there were striking

Table 10. Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release. Ephemeroptera and Plecoptera were all nymphs; Megaloptera, Trichoptera, and Diptera were larvae except for occasional pupae; Coleoptera were either larvae (l) or adults (a); and Acari and Bivalvia were adults.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Ephemeroptera	90.8	14.6	25.2	7.76	67.7	17.1
Ameletidae	5.33	2.96	0.667	0.667	0	0
Ameletus sp.	5.33	2.96	0.667	0.667	0	0
Baetidae	16.8	5.77	11.5	3.73	48.2	13.9
Baetis spp.	16.8	5.77	11.3	3.69	48.2	13.9
Unknown	0	0	0.167	0.167	0	0
Heptageniidae	10.3	4.86	2.00	0.775	1.50	0.563
Cinygmula sp.	2.67	1.02	0.167	0.167	1.17	0.601
Epeorus longimanus	3.67	1.98	0.500	0.342	0	0
Epeorus sp.	0.500	0.500	0.167	0.167	0	0
Ironodes sp.	3.50	2.63	1.17	0.543	0.333	0.21
Ephemerellidae	21.7	5.71	5.00	3.46	0.167	0.167
Caudatella hystrix	1.83	1.05	0.833	0.543	0	0
Ephemerella excrucians	5.33	1.61	1.33	1.151	0	0
Ephemerella dorothea infrequens	7.50	4.75	2.33	1.94	0	0
Ephemerella sp. A	0.500	0.500	0.500	0.500	0	0
Serratella teresa	6.50	0.719	0	0	0	0
Serratella micheneri	0	0	0	0	0.167	0.167

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Leptophlebiidae	36.7	7.38	6.00	3.12	17.8	16.1
Paraleptophlebia sp. A	35.5	6.78	5.67	3.03	4.00	2.71
Paraleptophlebia sp. B	1.17	1.17	0.333	0.333	13.8	13.4
Plecoptera	86.2	25.9	15.7	5.48	16.8	4.62
Nemouridae	73.2	25.7	10.8	4.23	13.8	3.94
Malenka sp.	73.2	25.7	10.8	4.23	13.8	3.94
Perlidae	9.50	2.94	2.50	0.619	1.33	0.615
Calineuria californica	0.333	0.211	0.667	0.667	0.333	0.333
Hesperoperla pacifica	9.17	2.94	1.33	0.715	0.833	0.654
Hesperoperla sp.	0	0	0.500	0.342	0.167	0.167
Perlodidae	3.00	0.775	0.667	0.211	0.333	0.333
Osobenus yakimae	3.00	0.775	0.667	0.211	0	0
Skwalla americana	0	0	0	0	0.333	0.333
Chloroperlidae	0.500	0.342	1.67	1.31	1.33	1.33
Haploperla chilnualna	0.167	0.167	0.167	0.167	1.33	1.33
Plumiperla sp.	0.167	0.167	1.17	1.17	0	0
Paraperla sp.	0.167	0.167	0	0	0	0
Suwallia sp. A	0	0	0.333	0.333	0	0

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Megaloptera	0.167	0.167	0.167	0.167	0	0
Corydalidae	0.167	0.167	0.167	0.167	0	0
Orohermes crepusculus	0.167	0.167	0.167	0.167	0	0
Trichoptera	10.0	2.31	8.00	2.35	18.2	5.96
Philopotamidae	0	0	0	0	1.00	0.632
Dolophilodes sp.	0	0	0	0	1.00	0.632
Polycentropodidae	1.17	0.980	1.33	1.15	3.50	2.50
Polycentropus sp.	1.17	0.980	1.33	1.15	3.50	2.50
Hydropsychidae	3.17	2.07	2.17	1.33	0	0
Hydropsyche sp.	3.17	2.07	2.17	1.33	0	0
Rhyacophilidae	2.17	0.703	1.00	0.516	0.833	0.307
Rhyacophila sp. A	1.50	0.563	0.667	0.494	0.500	0.224
Rhyacophila sp. B	0.167	0.167	0.333	0.211	0.167	0.167
Rhyacophila sp. C	0.167	0.167	0	0	0	0
Rhyacophila sp. D	0.333	0.333	0	0	0.167	0.167

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Hydroptilidae	2.67	0.954	1.83	0.703	11.7	5.18
Hydroptila sp. A	1.00	0.817	0	0	11.3	5.28
Hydroptila sp. B	1.50	0.806	1.83	0.703	0.167	0.167
Hydroptila sp. pupa	0.167	0.167	0	0	0.167	0.167
Lepidostomatidae	0.833	0.401	1.50	1.02	1.00	0.632
Lepidostoma sp.	0.833	0.401	1.50	1.02	1.00	0.632
Limnephilidae	0	0	0.167	0.167	0	0
Psychoglypha sp.	0	0	0.167	0.167	0	0
Coleoptera	2.83	1.01	0.833	0.401	2.17	0.703
Haliplidae	0	0	0	0	0.167	0.167
Haliplus sp. (a)	0	0	0	0	0.167	0.167
Dytiscidae	0.167	0.167	0.167	0.167	0.333	0.211
Hygrotus sp. (l)	0.167	0.167	0	0	0	0
Laccophilus sp. (a)	0	0	0	0	0.167	0.167
Neoclypeodytes sp. (l)	0	0	0.167	0.167	0	0
Uvarus sp. (a)	0	0	0	0	0.167	0.167
Hydraenidae	0.167	0.167	0	0	0	0
Hydraena sp. (a)	0.167	0.167	0	0	0	0

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Elmidae	2.50	0.957	0.667	0.422	1.67	0.558
Ampumixis sp. (l)	0.167	0.167	0	0	0	0
Cleptelmis addenda (l)	0.667	0.333	0	0	0.333	0.333
Cleptelmis addenda (a)	0.167	0.167	0	0	0	0
Optioservus quadrimaculatus (l)	0.500	0.224	0.167	0.167	0	0
Optioservus quadrimaculatus (a)	1.00	0.683	0.500	0.342	1.33	0.333
Diptera	892	260	61.0	21.2	310	112
Chironomidae*	879	257	57.0	20.6	291	107
Tanypodinae	123	24.1	27.0	10.6	33.5	10.6
Chironominae: Tanytarsini	90.3	18.3	6.5	3.68	21.7	9.51
Other Chironomidae	666	241	23.5	9.79	236	97.9
Simuliidae	4.00	1.61	1.17	0.401	13.5	6.19
Simulium spp.	4.00	1.61	1.17	0.401	13.5	6.19
Tipulidae	0.833	0.543	0.333	0.211	0.333	0.211
Antocha sp.	0.833	0.543	0.167	0.167	0	0
Dicranota sp.	0	0	0	0	0.167	0.167
Hexatoma sp.	0	0	0.167	0.167	0	0
Limonia sp.	0	0	0	0	0.167	0.167

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2008 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Empididae	7.83	4.43	2.50	0.847	4.17	2.02
Chelifera sp.	0.333	0.211	0.167	0.167	4.17	2.02
Clinocera sp.(l)	5.33	3.61	2.17	0.946	0	0
Clinocera sp. pupa	0.167	0.167	0	0	0	0
Hemerodromia sp.	2.00	1.00	0.167	0.167	0	0
Acari	2.17	1.08	0.833	0.477	0.167	0.167
Sperchontidae	2.17	1.08	0.833	0.477	0.167	0.167
Sperchon sp.	2.17	1.08	0.833	0.477	0.167	0.167
Bivalvia	2.00	1.18	0.833	0.833	0.667	0.422
Sphaeriidae	2.00	1.18	0.833	0.833	0.667	0.422
Sphaerium sp.	2.00	1.18	0.833	0.833	0.667	0.422
Total Individuals	**1086**	**287**	**112**	**33.6**	**415**	**123**

* Individual chironomid morphospecies were separated and counted but most were not identified

reductions in abundances for a number of families between the second and third samplings. Among mayflies, heptageniids were reduced in number, ephemerellids were almost eliminated, and ameletids were completely absent. Perlid, perlodid, and nemourid stoneflies were all reduced in number as were hydropsychid and rhyacophilid caddisflies (Table 10). Mean California tolerance value (Table 5) for families that reached highs two months after the release was 5.5 (SE= 0.50) but was 1.9 (SE= 0.55) for families that had reduced populations at this time.

Chironomids also dominated the 2009 assemblage but were not reduced in abundance after the release and increased greatly in abundance by two months after the flood receded (847/m^2; Table 11). Baetids were again abundant throughout the study and again reached their highest numbers two months after the release. As in 2008, simuliids were low in number until two months after the release, but unlike in 2008 the 09 increase was dramatic, and simuliids were the second most abundant family at this time (371/m^2; Table 11). Leptophlebiids were the third most abundant family in 2009 and showed similar responses to flooding as in 2008. Nemourids also had a similar response but had lower absolute and proportional abundance than in 2008. Ephemerellids were again speciose and moderately abundant in 2009, and both richness and abundance dropped after the release, but not as dramatically as in 2008 (Table 11).

In contrast to 2008, only one-third of the families had their highest abundances before the 2009 release, and 11 or 29 families were most abundant two months after the release (Table 11). Nine families were collected at their lowest densities after the 09 release, but four smaller families had highest abundances immediately after the

Table 11. Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release. Ephemeroptera and Plecoptera were all nymphs; Megaloptera, Trichoptera, and Diptera were larvae except for occasional pupae; Coleoptera were either larvae (l) or adults (a); and Acari and Bivalvia were adults.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Collembola	0	0	0.167	0.167	0	0
Isotomidae	0	0	0.167	0.167	0	0
Ephemeroptera	122	33.4	56.8	12.7	299	57.4
Ameletidae	0.50	0.34	0	0	0	0
Ameletus sp.	0.50	0.34	0	0	0	0
Baetidae	63.3	16.5	51.2	15.2	290	59.8
Baetis spp.	63.3	16.5	51.2	15.2	290	59.8
Heptageniidae	4.83	3.52	0.333	0.211	0	0
Cinygmula sp.	1.33	0.803	0.333	0.211	0	0
Epeorus longimanus	2.17	1.45	0	0	0	0
Ironodes sp.	1.33	1.33	0	0	0	0
Ephemerellidae	19.0	9.20	0.333	0.333	0.833	0.307
Ephemerella excrucians	12.0	6.64	0	0	0	0
Ephemerella dorothea infrequens	5.83	2.81	0	0	0	0
Ephemerella sp. A	0.500	0.342	0	0	0.167	0.167
Drunella spinifera	0	0	0	0	0.167	0.167

Table 11 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Ephemerellidae (cont.)						
Serratella teresa	0.500	0.342	0.333	0.333	0	0
Serratella sp.	0.167	0.167	0	0	0.167	0.167
Unknown	0	0	0	0	0.333	0.333
Leptophlebiidae	33.9	20.1	5.00	4.61	7.83	5.06
Paraleptophlebia sp. A	33.7	20.2	5.00	4.61	7.83	5.06
Paraleptophlebia sp. B	0.167	0.167	0	0	0	0
Plecoptera	27.2	15.0	12.5	4.19	12.0	3.42
Pteronarcyidae	0	0	0.167	0.167	0	0
Pteronarcys sp.	0	0	0.167	0.167	0	0
Nemouridae	22.3	13.3	9.50	3.24	9.00	2.45
Malenka sp.	22.3	13.3	9.50	3.24	9.00	2.45
Perlidae	1.50	1.03	2.00	0.856	2.17	1.45
Calineuria californica	0.667	0.422	0.167	0.167	0.667	0.333
Hesperoperla pacifica	0.833	0.654	1.83	0.910	1.50	1.31
Perlodidae	0.833	0.654	0.333	0.333	0.167	0.167
Osobenus yakimae	0.833	0.654	0	0	0	0
Skwalla americana	0	0	0.333	0.333	0.167	0.167

Table 11 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Plecoptera (cont.)						
Chloroperlidae	2.50	1.77	0.500	0.500	0.833	0.654
Haploperla chilnualna	1.67	0.989	0.500	0.500	0.667	0.494
Paraperla sp.	0.167	0.167	0	0	0	0
Suwallia sp. A	0.667	0.667	0	0	0.167	0.167
Megaloptera	0	0	0.167	0.167	0	0
Corydalidae	0	0	0.167	0.167	0	0
Orohermes crepusculus	0	0	0.167	0.167	0	0
Trichoptera	9.83	5.45	4.50	1.98	12.5	2.45
Polycentropodidae	0.833	0.543	1.33	1.33	1.17	1.17
Polycentropus sp.	0.833	0.543	1.33	1.33	1.17	1.17
Hydropsychidae	0.167	0.167	0.333	0.333	4.50	2.98
Hydropsyche sp.	0.167	0.167	0.333	0.333	4.50	2.98
Rhyacophilidae	1.67	0.667	2.33	1.48	0.667	0.333
Rhyacophila sp. A	1.33	0.558	0	0	0	0
Rhyacophila sp. B	0	0	1.83	1.47	0.167	0.167
Rhyacophila sp. C	0	0	0	0	0.167	0.167

Table 11 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Rhyacophilidae (cont.)						
Rhyacophila sp. D	0.333	0.211	0.500	0.342	0.167	0.167
Unknown (pupa)	0	0	0	0	0.167	0.167
Brachycentridae	0	0	0	0	0.167	0.167
Micrasema sp.	0	0	0	0	0.167	0.167
Hydroptilidae	0.500	0.224	0.167	0.167	5.00	1.69
Hydroptila sp. A (l)	0	0	0.167	0.167	4.67	1.50
Hydroptila sp. A (pupa)	0	0	0	0	0.333	0.333
Hydroptila sp. B	0.500	0.224	0	0	0	0
Lepidostomatidae	5.83	3.55	0.167	0.167	1.00	0.516
Lepidostoma sp.	5.83	3.55	0.167	0.167	1.00	0.516
Limnephilidae	0.833	0.654	0.167	0.167	0	0
Psychoglypha sp.	0.667	0.667	0.167	0.167	0	0
Unknown	0.167	0.167	0	0	0	0
Coleoptera	2.33	1.94	0.833	0.477	2.33	1.59
Dytiscidae	0	0	0	0	0.333	0.211
Neoclypeodytes sp. (l)	0	0	0	0	0.333	0.211

Table 11 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release.

	Before		**After**		**2 months after**	
	Mean	SE	Mean	SE	Mean	SE
Coleoptera (cont.)						
Elmidae	2.33	1.94	0.833	0.477	2.00	1.61
Cleptelmis addenda (l)	1.83	1.83	0.500	0.500	1.67	1.48
Heterlimnius sp.	0	0	0.167	0.167	0	0
Optioservus quadrimaculatus (l)	0	0	0	0	0.167	0.167
Optioservus quadrimaculatus (a)	0.500	0.224	0.167	0.167	0.167	0.167
Diptera	229	51.4	246	56.4	1221	213
Chironomidae*	218	52.0	238	56.1	847	253
Tanypodinae	4.17	4.17	25.5	15.1	55.0	16.4
Chironominae: Tanytarsini	35.0	12.3	18.0	12.7	71.0	23.2
Other Chironomidae	179	38.5	194	39.3	721	217
Simuliidae	5.17	1.76	3.00	1.03	371	146
Simulium spp. (l)	5.00	1.71	2.83	1.01	362	141
Simulium spp. (pupa)	0.167	0.167	0.167	0.167	9.33	7.07
Tipulidae	0	0	0.167	0.167	0.333	0.333
Dicranota sp.	0	0	0.167	0.167	0	0
Hexatoma sp.	0	0	0	0	0.333	0.333

Table 11 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 2009 experimental release.

	Before		**After**		**2 months after**	
Diptera (contd.)	Mean	SE	Mean	SE	Mean	SE
Empididae	5.00	1.77	4.33	1.73	4.00	1.61
Chelifera sp. (l)	2.00	1.03	2.00	0.817	1.67	0.803
Chelifera sp. (pupa)	0.167	0.167	0	0	1.50	0.671
Clinocera sp.	2.50	0.957	2.33	1.20	0.333	0.211
Neoplasta sp.	0	0	0	0	0.500	0.342
Wiedemannia sp.	0.333	0.333	0	0	0	0
Acari	0.333	0.333	0	0	0	0
Limnesiidae	0.333	0.333	0	0	0	0
Bivalvia	1.33	1.33	0	0	0	0
Sphaeriidae	1.33	1.33	0	0	0	0
Sphaerium sp.	1.33	1.33	0	0	0	0
Total Individuals	**390**	**89.5**	**321**	**55.0**	**1547**	**231**

* Individual chironomid morphospecies were separated and counted but most were not identified.

release. The latter did not include Chloroperlidae and Lepidostomatidae in 2009. Amelitid and heptageniid mayflies, perlodid stoneflies, limnephilid caddisflies, mites, and clams were all absent or almost absent two months after the 2009 release (Table 11). Tolerance values were again in general higher for taxa that flourished two months after the release than for those taxa that were greatly reduced in number.

Functional feeding groups were also apparently affected by the experimental release. In 2008, the proportional contribution of collector-gatherers decreased, and all other groups increased, after the release (Table 12). The opposite relationship generally held in 2009. By two months after the 2008 release, proportion of collector-gatherers approximated pre-release levels, and most other groups fell in turn. Collector-filterers and piercer-herbivores, however, retained proportions similar to those observed after the release (Table 12). In 2009, by two months after the release, most feeding groups dropped in proportion, including collector gatherers, but collector-filterers increased from one percent to 28% of the assemblage. The proportions of scrapers, shredders, and piercer-herbivores were all higher in 2008 than in 2009.

Drift response to changing flow

Temperature was lowest during water level rise (Table 13). Hourly changes in depth were less for comparisons as a function of hydrographic limb, regardless of change or lack thereof within a given net set, versus *post hoc* comparison of changes within individual net sets, regardless of timing relative to overall hydrographic limb.

Most assemblage metrics differed significantly as a function of hydrographic limb

Table 12. Response of functional feeding groups to the 2008 and 2009 experimental release (all per-square-meter). %EPT= percent Ephemeroptera + Plecoptera + Trichoptera. "Sampling" references differences among the Before, After, and Two months after sampling periods. * represents p< 0.05; ** represents p< 0.01.

	Year	**Before**		**After**		**2 mo after**		**ANOVA**		
		$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	**Sampling**	**Year**	**Sampling * Year**
% Scrapers	08	1.90	0.640	2.54	0.946	0.546	0.182	0.012*	0.013*	0.16
	09	1.09	0.555	0.127	0.093	0.000	0.000			
% Predators	08	2.96	0.596	12.1	3.66	3.67	1.11	0.0024**	0.46	0.015*
	09	10.9	3.48	9.63	3.22	3.90	0.889			
% Collector-Gatherers	08	86.8	1.48	65.5	5.49	82.1	4.72	0.36	0.78	0.039*
	09	79.9	4.66	86.3	3.90	67.1	10.6			
% Shredders	08	7.57	1.09	11.1	2.73	5.86	1.89	0.0027**	0.021*	0.084
	09	6.15	2.65	2.83	0.850	0.672	0.183			
% Collector-Filterers	08	0.670	0.193	4.48	1.74	4.77	1.69	0.0013**	0.20	0.013*
	09	1.85	0.878	1.09	0.390	28.2	11.6			
%Piercer-Herbivores	08	0.354	0.155	3.61	2.39	3.28	1.31	0.13	0.0012**	0.25
	09	0.092	0.043	0.094	0.094	0.306	0.089			

Table 13. Means and standard errors for physical parameters as a function of discharge at netting location at the scale of hydrographic limbs and individual net sets. * represents $p< 0.05$ for 1x3 ANOVA. Superscripts represent pairs of means that were not significantly different via independent t-tests. Tests were not possible at the scale of individual net sets due to small sample sizes for some factors.

	Falling		**Reference**		**Rising**		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Change by Limb							
Depth change (cm)	-2.00	1.2	+0.38	0.38	+2.83	1.9	0.10
Temp (°C)	$9.10^{1,2}$	0.38	11.1^{1}	1.4	8.58^{2}	0.12	0.031*
Change During Sets							
Depth change (cm)	-5.03	0.025	+0.141	0.152	+8.50	2.00	
Temp (°C)	9.63	0.375	9.38	0.537	8.63	0.375	

(Table 14). Although overall densities did not differ significantly across limbs (p= 0.083), densities were lowest for reference discharge. Overall aquatic and terrestrial drift densities were also lowest during reference conditions. Aquatic organisms were densest during falling limbs, and terrestrial fauna were densest on rising limbs. Aquatic fauna were almost ten times as dense during falling limbs as during reference conditions (Table 14). Terrestrial fauna during rises were eight times denser than during falling limbs, and percent of terrestrial fauna was also low in falling limbs. Expected number of families was highest for reference conditions and lowest during rises (Table 14). Expected number of species and PIE did not differ significantly (p= 0.070 and 0.42, respectively), but the trends were to that of expected number of families. In turn, family and species dominance were highest during rising hydrographic limbs (Table 14). The rank-abundance plots indicate somewhat less evenness for the falling limb; strong dominance among the most abundant families is indicated for the rising limb (Fig. 21).

We identified 3,934 organisms representing 17 orders and 118 families (Table 15). Eighty-three families were exclusively terrestrial. Many of the remainder had both aquatic and terrestrial life history stages, typically aquatic larvae or nymphs and terrestrial adults (Table 15). We often collected both aquatic and adult forms; example families included baetid and ephemerellid mayflies, nemourid and chloroperlid stoneflies, hydrophilid and elmid beetles, polycentropid and hydroptilid caddisflies, and tipulid, ceratopogonid, chironomid, simuliid, and empidid flies. Diptera, Ephemeroptera, Hemiptera, and Hymenoptera were the most common orders in the drift (Table 15). The most abundant families were Chironomidae (mostly collected as terrestrial adults),

Table 14. Means and standard errors for drift assemblage metrics by hydrographic limb with results of 1x3 ANOVAs and t-tests. T-tests were only performed when there was a significant ANOVA result. Identical superscripts for a pair of means indicates the lack of a significant t-test difference. * and ** flag differences that were significant at p< 0.05 and p< 0.01, respectively.

	Falling		**Reference**		**Rising**		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
# individuals/100m^3	187	59	80.7	17	283	72	0.083
Aquatic # individuals/100m^3	158	56	16.5[1]	11	76.2[1]	15	0.0097**
Terrestrial # inds./100m^3	28.6	5.9	64.2	17	207	59	0.021*
% Terrestrial animals	25.8	8.5	80.7[1]	11	71.1[1]	2.9	0.00039**
Expected no. of families	17.6	1.7	23.9	2.1	13.3	2.4	0.017*
Expected no. of species	29.0	3.0	38.0	2.4	26.0	3.6	0.070
PIE	0.940	0.0067	0.936	0.013	0.897	0.035	0.42
% Family dominance	25.6[1]	2.3	30.9[1]	9.0	58.2	4.5	0.0014**
% Species dominance	13.4	1.7	19.0	4.2	20.4	6.2	0.56

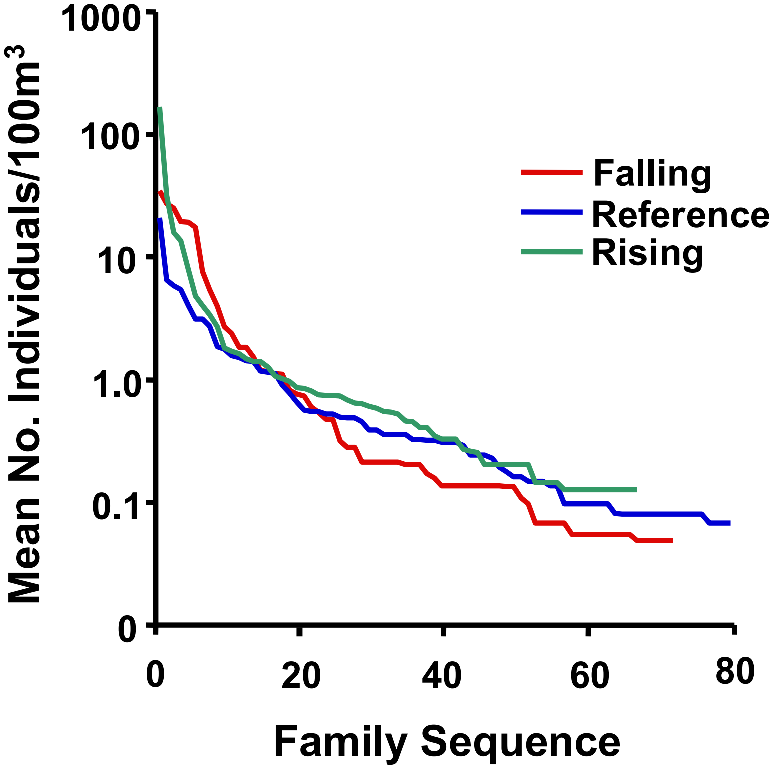

Fig. 21. Rank-abundance plots for drift fauna as a function of hydrograph limb.

Table 15. Means and standard errors for drift population metrics by hydrographic limb with results of 1x3 ANOVAs and t-tests for higher taxonomic levels and the ten most abundant life forms. T-tests were only performed when there was a significant ANOVA result. Identical superscripts for a pair of means indicates the lack of a significant t-test difference. * and ** flag differences that were significant at $p< 0.05$ and $p< 0.01$, respectively. **Bold** indicates terrestrial. n= nymph, l= larva, p= pupa, a= adult.

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Collembola	0.0554	0.055	0.0807	0.081	0.330	0.22	0.40
Isotomidae (a)	0.0	0.0	0.0807	0.081	0.330	0.22	
Unknown nymph	0.0554	0.055	0.0	0.0	0.0	0.0	
Ephemeroptera	78.5^{1}	31	9.71	6.0	36.3^{1}	9.4	0.050*
Ameletidae (n)	0.204	0.14	0.0	0.0	0.0	0.0.	
Baetidae (n)	17.1	6.4	5.93	5.2	28.6	9.0	0.16
Baetidae (a)	0.443	0.31	0.604	0.23	3.13	1.1	
Ephemerellidae (n)	27.5	14	0.136^{1}	0.14	1.21^{1}	0.61	0.011*
Ephemerellidae (a)	0.0	0.0	1.63	1.5	0.203	0.20	
Heptageniidae (n)	25.0	11	0.0^{1}	0.0	0.407^{1}	0.27	0.00066**
Leptophlebiidae (n)	7.05	3.2	0.717	0.717	0.590	0.38	
Leptophlebiidae (a)	0.594	0.39	0.701	0.27	2.10	0.97	
Siphlonuridae (n)	0.137	0.14	0.0	0.0	0.0	0.0	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Odonata	0.766	0.50	0.0	0.0	0.254	0.25	0.33
Aeschnidae (n)	0.766	0.50	0.0	0.0	0.127	0.13	
Coenagrionidae (n)	0.0	0.0	0.0	0.0	0.127	0.13	
Plecoptera	23.8	11	0.617[1]	0.30	1.09[1]	0.78	0.033*
Taniopterygidae (n)	0.137	0.14	0.0	0.0	0.0	0.0	
Nemouridae (n)	19.6	8.9	0.456[1]	0.34	0.551[1]	0.40	0.0056**
Nemouridae (a)	0.0	0.0	0.0	0.0	0.203	0.20	
Perlidae (n)	3.98	1.8	0.0	0.0	0.0	0.0	
Chloroperlidae (n)	0.135	0.14	0.0	0.0	0.127	0.13	
Chloroperlidae (a)	0.0	0.0	0.161	0.16	0.203	0.20	
Hemiptera	4.59	1.9	8.04	2.2	16.7	7.6	0.29
Gerridae (n)	1.13	0.57	0.292	0.29	0.864	0.61	
Corixidae (n)	0.054	0.054	0.0	0.0	0.127	0.13	
Miridae (n,a)	0.054	0.054	0.391	0.31	0.854	0.50	
Nabidae (a)	0.0	0.0	0.068	0.068	0.0	0.0	
Anthocoridae (a)	0.0	0.0	0.081	0.081	0.0	0.0	
Rhyparochromidae (a)	0.054	0.054	0.149	0.086	0.0	0.0	
Lygaeidae (a)	0.0	0.0	0.565	0.57	0.0	0.0	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Cicadellidae (n,a)	0.171	0.072	0.526	0.32	0.457	0.29	
Delphacidae (a)	0.213	0.21	0.0	0.0	0.203	0.20	
Psyllidae (a)	0.0	0.0	0.068	0.07	0.0	0.0	
Aphididae (n, a)	2.71	2.07	5.41	2.09	13.5	6.3	0.24
Unknown nymph	0.204	0.14	0.494	0.34	0.610	0.29	
Thysanoptera	0.204	0.14	3.11	2.1	0.145	0.15	0.10
Thripidae (a)	0.204	0.14	3.11	2.1	0.145	0.15	
Psocoptera	0.109	0.11	0.458	0.31	0.0	0.0	0.14
Caeciliusidae (n,a)	0.109	0.11	0.0	0.0	0.0	0.0	
Lachesillidae (a)	0.0	0.0	0.242	0.24	0.0	0.0	
Psocidae (a)	0.0	0.0	0.081	0.081	0.0	0.0	
Unknown nymph	0.0	0.0	0.136	0.14	0.0	0.0	
Coleoptera	2.90	0.73	3.11	1.4	6.11	2.04	0.31
Dytiscidae (a)	0.213	0.21	0.0	0.0	0.127	0.13	
Hydrophilidae (l)	0.0	0.0	0.081	0.081	0.348	0.23	
Hydrophilidae (a)	0.213	0.21	0.0	0.0	0.290	0.29	
Hydraenidae (a)	0.0	0.0	0.242	0.24	0.0	0.0	
Ptiliidae (a)	0.0	0.0	0.242	0.24	0.0	0.0	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Staphylinidae (a)	0.603	0.40	1.14	0.34	1.72	0.82	
Elmidae (l)	0.152	0.10	0.0	0.0	0.684	0.34	
Elmidae (a)	1.39	0.50	0.0	0.0	0.0	0.0	
Elateridae (a)	0.0	0.0	0.0	0.0	0.742	0.47	
Cantharidae (a)	0.049	0.049	0.068	0.068	0.585	0.40	
Dermestidae (a)	0.0	0.0	0.097	0.097	0.0	0.0	
Bostrichidae (a)	0.0	0.0	0.0	0.0	0.551	0.40	
Anobiidae (a)	0.0	0.0	0.229	0.15	0.127	0.13	
Cleridae (a)	0.0	0.0	0.0	0.0	0.203	0.20	
Cucujidae (a)	0.0	0.0	0.097	0.097	0.0	0.0	
Phalacridae (a)	0.0	0.0	0.081	0.081	0.203	0.20	
Erotylidae (a)	0.0	0.0	0.0	0.0	0.127	0.13	
Coccinellidae (a)	0.0	0.0	0.097	0.097	0.0	0.0	
Latridiidae (a)	0.0	0.0	0.552	0.47	0.0	0.0	
Anthicidae (a)	0.0	0.0	0.081	0.081	0.254	0.25	
Cerambycidae (a)	0.049	0.049	0.0	0.0	0.0	0.0	
Chrysomelidae (a)	0.098	0.098	0.0	0.0	0.145	0.15	
Brentidae (a)	0.213	0.21	0.0	0.0	0.0	0.0	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Neuroptera	0.103	0.063	0.0	0.0	0.0	0.0	0.11
Raphidiidae (a)	0.049	0.049	0.0	0.0	0.0	0.0	
Inocelliidae (a)	0.054	0.054	0.0	0.0	0.0	0.0	
Hymenoptera	4.62	1.4	10.3	3.5	14.7	5.1	0.22
Xyelidae (a)	0.0	0.0	0.0	0.0	0.145	0.15	
Pamphiliidae (a)	0.213	0.21	0.0	0.0	0.0	0.0	
Cimbicidae (a)	0.0	0.0	0.0	0.0	0.203	0.20	
Tenthredinidae (a)	0.0	0.0	0.0	0.0	0.127	0.13	
Megaspilidae (a)	0.0	0.0	0.081	0.081	0.262	0.26	
Ceraphronidae (a)	0.068	0.068	0.526	0.32	0.0	0.0	
Braconidae (a)	0.280	0.15	1.18	0.62	1.64	1.0	
Ichneumonidae (a)	0.0	0.0	0.552	0.47	0.0	0.0	
Mymaridae (a)	0.049	0.049	0.149	0.086	0.0	0.0	
Eulophidae (a)	0.068	0.068	0.194	0.19	0.0	0.0	
Encyrtidae (a)	0.0	0.0	0.655	0.30	0.0	0.0	
Eupelmidae (a)	0.137	0.14	0.323	0.32	0.0	0.0	
Torymidae (a)	0.0	0.0	0.178	0.10	0.0	0.0	
Pteromalidae (a)	0.472	0.18	1.58	1.1	0.737	0.60	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Perilampidae (a)	0.068	0.068	0.310	0.23	0.330	0.22	
Eucoilidae (a)	0.0	0.0	0.323	0.32	1.02	1.02	
Cynipidae (a)	0.0	0.0	0.136	0.14	0.969	0.51	
Proctotrupidae (a)	0.0	0.0	0.081	0.081	0.0	0.0	
Diapriidae (a)	0.213	0.21	0.326	0.13	0.0	0.0	
Scelionidae (a)	0.0	0.0	1.12	0.55	0.0	0.0	
Platygastridae (a)	0.543	0.40	0.326	0.13	1.26	0.47	
Embolemidae (a)	0.049	0.049	0.358	0.36	0.0	0.0	
Pemphredonidae (a)	0.054	0.054	0.0	0.0	0.0	0.0	
Apidae (a)	0.0	0.0	0.0	0.0	0.127	0.13	
Formicidae (a)	2.41	0.87	1.86	0.21	7.86	3.0	
Trichoptera	7.04	2.9	1.24	1.03	3.99	1.8	0.14
Hydropsychidae (l)	1.20	0.51	0.358	0.36	0.0	0.0	
Polycentropodidae (l)	1.79	1.3	0.0	0.0	1.70	1.1	
Polycentropodidae (a)	0.054	0.054	0.0	0.0	0.127	0.13	
Philopotamidae (l)	0.0	0.0	0.081	0.081	0.0	0.0	
Hydroptilidae (l)	0.0	0.0	0.0	0.0	0.127	0.13	
Hydroptilidae (a)	0.738	0.62	0.081	0.081	0.145	0.15	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Rhyacophilidae (l)	1.16	0.60	0.0	0.0	0.0	0.0	
Limnephilidae (l)	0.135	0.14	0.0	0.0	0.406	0.41	
Lepidostomatidae (l)	1.83	0.59	0.358	0.36	1.48	0.53	
Leptoceridae (l)	0.137	0.14	0.358	0.36	0.0	0.0	
Lepidoptera	0.0	0.0	0.081	0.081	0.127	0.13	0.63
Coleophoridae (a)	0.0	0.0	0.081	0.081	0.0	0.0	
Gelechiidae (a)	0.0	0.0	0.0	0.0	0.127	0.13	
Diptera	57.3[1]	20	36.6[1]	7.0	201	57	0.010*
Tipulidae (l)	0.068	0.068	0.0	0.0	0.0	0.0	
Tipulidae (a)	0.0	0.0	0.0	0.0	0.127	0.13	
Psychodidae (a)	0.0	0.0	0.081	0.081	0.348	0.23	
Ceratopogonidae (p)	0.213	0.21	0.0	0.0	0.0	0.0	
Ceratopogonidae (a)	0.603	0.26	3.11	1.3	3.40	2.2	
Chironomidae (l)	16.1[1]	6.5	2.91	1.6	17.4[1]	5.2	0.031*
Chironomidae (p)	5.34[1]	2.4	4.04[1]	1.3	15.2	3.2	0.027*
Chironomidae (a)	13.5[1]	4.4	13.9[1]	3.1	135	47	0.0056**
Culicidae (a)	0.0	0.0	0.081	0.081	0.0	0.0	
Simuliidae (l)	19.2	9.0	1.20	0.72	4.61	2.9	0.071

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Simuliidae (a)	0.171	0.072	0.310	0.23	0.203	0.20	
Deuterophlebiidae (a)	0.0	0.0	0.161	0.16	0.0	0.0	
Bibionidae (a)	0.0	0.0	0.391	0.31	0.0	0.0	
Cecidomyiidae (a)	0.281	0.21	1.43	0.59	0.748	0.34	
Mycetophilidae (a)	0.137	0.14	0.149	0.086	0.813	0.81	
Scatopsidae (a)	0.0	0.0	0.0	0.0	0.527	0.38	
Sciaridae (a)	1.11	0.69	4.01	1.4	4.00	2.0	
Bombyliidae (a)	0.0	0.0	0.097	0.097	0.0	0.0	
Empididae (l)	0.068	0.068	0.0	0.0	0.0	0.0	
Empididae (a)	0.410	0.41	2.74	2.2	0.643	0.42	
Phoridae (a)	0.0	0.0	0.488	0.28	0.0	0.0	
Anthomyiidae (a)	0.054	0.054	0.0	0.0	0.0	0.0	
Muscidae (a)	0.0	0.0	0.0	0.0	0.203	0.20	
Sphaeroceridae (a)	0.0	0.0	0.904	0.55	1.07	0.80	
Drosophilidae (a)	0.137	0.14	0.0	0.0	0.0	0.0	
Ephydridae (a)	0.158[1]	0.11	0.488[1]	0.28	15.9	5.3	0.000049**
Unknown larvae	0.0	0.0	0.097	0.097	0.463	0.33	
Unknown adult	0.0	0.0	0.0	0.0	0.127	0.13	

	Falling		**Reference**		**Rising**		ANOVA
	Mean	SE	Mean	SE	Mean	SE	
Araneae	0.756	0.37	6.57	3.0	1.95	1.1	0.071
Araneidae (a)	0.213	0.21	0.310	0.23	0.0	0.0	
Linyphiidae (a)	0.317	0.20	5.86	2.8	1.41	1.1	
Cybaeidae (a)	0.068	0.068	0.0	0.0	0.0	0.0	
Lycosidae (a)	0.054	0.054	0.0	0.0	0.0	0.0	
Gnaphosidae (a)	0.049	0.049	0.0	0.0	0.0	0.0	
Thomisidae (a)	0.0	0.0	0.310	0.23	0.0	0.0	
Salticidae (a)	0.054	0.054	0.097	0.097	0.548	0.55	
Acari	5.56^{1}	2.8	0.853^{1,2}	0.68	0.406^{2}	0.41	0.042*
Limnesiidae (a)	5.421	2.8	0.785	0.70	0.203	0.20	
Caeculidae (a)	0.0	0.0	0.068	0.068	0.0	0.0	
Oribatei (a)	0.137	0.14	0.0	0.0	0.0	0.0	
Unknown larva	0.0	0.0	0.0	0.0	0.203	0.20	
Nematomorpha (a)	0.137	0.14	0.0	0.0	0.0	0.0	0.40
Oligochaeta (a)	0.0	0.0	0.0	0.0	0.145	0.15	0.51

Baetidae (mostly nymphs), Aphidae (aphids), and Simuliidae (mostly larvae). The orders with the greatest numbers of families were Hymenoptera (25, all terrestrial), Coleoptera (20, mostly terrestrial), and Diptera (19, mostly terrestrial).

The highest densities for individual aquatic taxa tended to occur during falling limbs, and the highest densities of terrestrial taxa often occurred during rising limbs (Table 15). This trend was significant for non-incidental (density> 1/100m^3) aquatic taxa (sign test, p= 0.0021) but not for terrestrial taxa (p= 0.076). Examples of strong trends included Ephemeroptera, ephemerellid and heptageniid mayfly nymphs, Plecoptera, and nemourid stonefly nymphs, but this pattern was not exhibited by other common aquatic taxa, such as baetid mayflies, Trichoptera, and chironomid larvae and pupae. Chironomid adults and ephydrid shore flies showed strong tendencies for appearing in the drift during rising limbs (Table 15).

When assemblage metrics were examined as a function of proximate changes in discharge, i.e., during individual sets, versus at the scale of hydrographic limbs, there were many similarities in response to discharge, but some differences emerged as well (Table 16). Trends for total individual and terrestrial densities showed an even stronger positive response to rising discharge, and percent terrestrial organisms and family dominance were again high during rises. Densities of aquatic fauna were again highest with falling discharge, though this trend was less strong than for the trends observed on the longer time scale (Table 16). Little trend was observed across discharge categories for expected number of families or species, or species dominance. Both PIE (Table 16) and rank-abundance plots (Fig. 22) suggested greater evenness with increasing discharge.

Table 16. Means and standard errors for drift assemblage metrics as a function of discharge changes during individual net sets. Tests were not advisable due to some small sample sizes.

	Falling		**Reference**		**Rising**	
	Mean	SE	Mean	SE	Mean	SE
# individuals/100m^3	156	101	167	34	402	205
Aquatic # individuals/100m^3	118	90	78.3	30	108	30
Terrestrial # inds./100m^3	37.5	11	88.9	24	294	175
% Terrestrial animals	33.9	15	61.2	9.2	68.9	8.4
Expected no. of families	18.1	1.9	17.5	2.2	17.5	3.1
Expected no. of species	29.9	2.1	29.9	3.0	32.2	3.8
PIE	0.938	0.0040	0.914	0.020	0.951	0.010
% Family dominance	26.55	0.22	40.2	6.2	52.8	5.9
% Species dominance	15.4	2.9	19.2	3.6	11.5	0.99

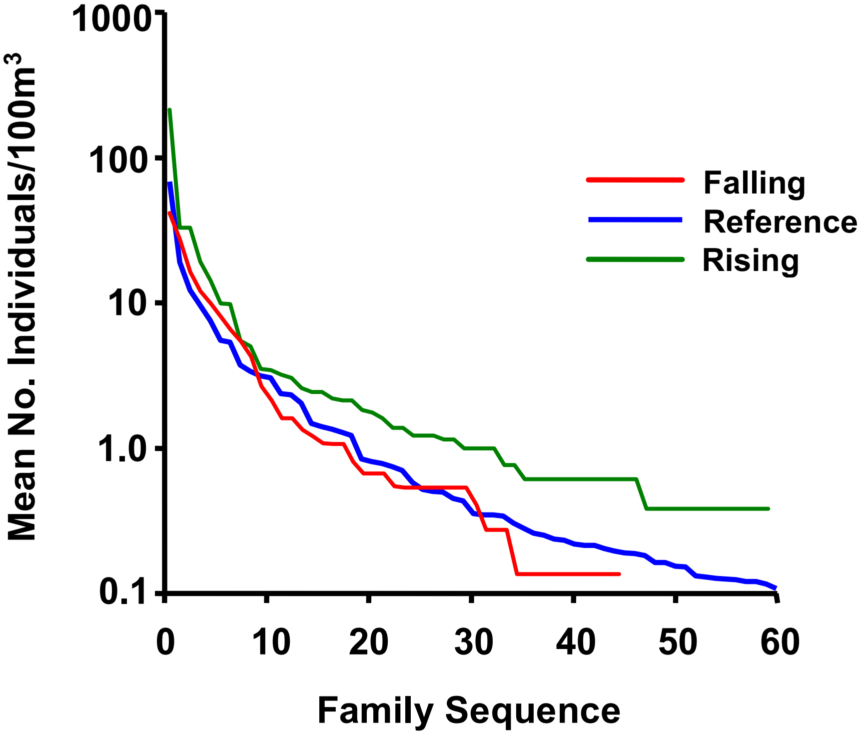

Fig. 22. Rank-abundance plots for drift fauna as a function of discharge changes within net sets. Reference curve was truncated due to larger sample size.

Similarly, population level data revealed both similarities and differences between trends at the scales of hydrographic limbs and net sets (Table 17). The latter showed no trend for increases in individual aquatic taxa abundances with falling discharge (sign test, p= 1.0), but the trend of larger numbers of terrestrial taxa in the drift during discharge increases was much stronger. Twenty-eight of 33 non-incidental terrestrial taxa showed this trend (sign test, p= 0.00013). Common terrestrial taxa for which drift densities were five or more times greater than reference or falling discharge included: baetid mayfly adults, cicadellid leafhoppers, aphids, elaterid click beetles, cantharid soldier beetles, bostrichid beetles, perilampid, eucolid, and cynipid wasps, mycetophilid fungus gnats, scatopsid scavenger flies, sphaerocerid dung flies, and ephydrid shore flies (Table 17).

Table 17. Means and standard errors for drift orders and families (individuals/100m^3) as a function of discharge changes during individual net sets. **Bold** indicates terrestrial. n= nymph, l= larva, p= pupa, a= adult.

	Falling		**Reference**		**Rising**	
	Mean	SE	Mean	SE	Mean	SE
Collembola	0.136	0.14	0.0293	0.029	0.991	0.23
Isotomidae (a)	0.0	0.0	0.0293	0.029	0.991	0.23
Unknown nymph	0.136	0.14	0.0	0.0	0.0	0.0
Ephemeroptera	43.7	31	43.6	17	40.8	26
Ameletidae (n)	0.0	0.0	0.0928	0.067	0.0	0.0
Baetidae (n)	15.5	11	17.8	5.5	26.9	23
Baetidae (a)	0.817	0.82	0.898	0.32	5.95	1.4
Ephemerellidae (n)	8.01	6.9	11.4	7.3	1.83	1.8
Ephemerellidae (a)	0.0	0.0	0.593	0.56	0.609	0.61
Heptageniidae (n)	12.0	10	9.41	6.1	0.0	0.0
Leptophlebiidae (n)	5.50	3.5	4.64	2.8	1.00	1.0
Leptophlebiidae (a)	1.49	0.42	0.541	0.29	4.73	0.15
Siphlonuridae (n)	0.0	0.0	0.0621	0.062	0.0	0.0
Odonata	0.136	0.14	0.324	0.25	0.763	0.76
Aeschnidae (n)	0.136	0.14	0.324	0.25	0.382	0.38

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Coenagrionidae (n)	0.0	0.0	0.0	0.0	0.382	0.38
Plecoptera	12.0	10	8.95	5.8	2.82	2.1
Taniopterygidae (n)	0.0	0.0	0.0621	0.062	0.0	0.0
Nemouridae (n)	9.88	8.3	7.34	4.8	1.22	1.2
Nemouridae (a)	0.0	0.0	0.0	0.0	0.609	0.61
Perlidae (n)	2.03	2.1	1.42	0.96	0.0	0.0
Chloroperlidae (n)	0.0	0.0	0.0616	0.062	0.382	0.38
Chloroperlidae (a)	0.0	0.0	0.0587	0.059	0.609	0.61
Hemiptera	8.12	3.9	5.47	1.5	39.3	5.8
Gerridae (n)	1.60	1.6	0.328	0.16	2.59	1.1
Corixidae (n)	0.136	0.14	0.0	0.0	0.382	0.38
Miridae (n,a)	0.136	0.14	0.428	0.30	0.991	0.23
Nabidae (a)	0.0	0.0	0.0247	0.025	0.0	0.0
Anthocoridae (a)	0.0	0.0	0.0293	0.029	0.0	0.0
Rhyparochromidae (a)	0.6	0.14	0.0540	0.036	0.0	0.0
Lygaeidae (a)	0.0	0.0	0.205	0.21	0.0	0.0
Cicadellidae (n,a)	0.136	0.14	0.244	0.13	1.37	0.15
Delphacidae (a)	0.136	0.14	0.0	0.0	0.609	0.61

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Psyllidae (a)	0.0	0.0	0.0247	0.025	0.0	0.0
Aphididae (n,a)	5.44	5.4	3.64	1.2	32.8	3.8
Unknown nymph	0.0	0.0	0.495	0.18	0.609	0.61
Thysanoptera	0.0	0.0	1.30	0.83	0.0	0.0
Thripidae (a)	0.0	0.0	1.30	0.83	0.0	0.0
Psocoptera	0.272	0.27	0.167	0.12	0.0	0.0
Caeciliusidae (n,a)	0.272	0.27	0.0	0.0	0.0	0.0
Lachesillidae (a)	0.0	0.0	0.0880	0.088	0.0	0.0
Psocidae (a)	0.0	0.0	0.0293	0.029	0.0	0.0
Unknown nymph	0.0	0.0	0.0493	0.049	0.0	0.0
Coleoptera	3.48	1.9	2.96	0.63	12.0	1.4
Dytiscidae (a)	0.0	0.0	0.0621	0.062	0.382	0.38
Hydrophilidae (l)	0.0	0.0	0.109	0.082	0.609	0.61
Hydrophilidae (a)	0.533	0.53	0.158	0.16	0.0	0.0
Hydraenidae (a)	0.0	0.0	0.0880	0.088	0.0	0.0
Ptiliidae (a)	0.0	0.0	0.0880	0.088	0.0	0.0
Staphylinidae (a)	1.34	0.80	0.745	0.32	3.51	1.1
Elmidae (l)	0.136	0.14	0.307	0.19	0.609	0.61

	Falling		**Reference**		**Rising**	
	Mean	SE	Mean	SE	Mean	SE
Elmidae (a)	0.942	0.13	0.494	0.31	0.0	0.0
Elateridae (a)	0.0	0.0	0.183	0.18	1.22	1.2
Cantharidae (a)	0.0	0.0	0.0469	0.032	1.75	0.54
Dermestidae (a)	0.0	0.0	0.0354	0.035	0.0	0.0
Bostrichidae (a)	0.0	0.0	0.0792	0.079	1.22	1.2
Anobiidae (a)	0.0	0.0	0.0834	0.061	0.382	0.38
Cleridae (a)	0.0	0.0	0.0	0.0	0.609	0.61
Cucujidae (a)	0.0	0.0	0.0354	0.035	0.0	0.0
Phalacridae (a)	0.0	0.0	0.0293	0.029	0.609	0.61
Erotylidae (a)	0.0	0.0	0.0	0.0	0.382	0.38
Coccinellidae (a)	0.0	0.0	0.0354	0.035	0.0	0.0
Latridiidae (a)	0.0	0.0	0.201	0.18	0.0	0.0
Anthicidae (a)	0.0	0.0	0.0293	0.029	0.763	0.76
Cerambycidae (a)	0.0	0.0	0.0223	0.022	0.0	0.0
Chrysomelidae (a)	0.0	0.0	0.124	0.087	0.0	0.0
Brentidae (a)	0.533	0.53	0.0	0.0	0.0	0.0
Neuroptera	0.136	0.14	0.0223	0.022	0.0	0.0
Raphidiidae (a)	0.0	0.0	0.0223	0.022	0.0	0.0

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Inocelliidae (a)	0.136	0.14	0.0	0.0	0.0	0.0
Hymenoptera	6.02	3.6	7.93	2.3	26.5	2.8
Xyelidae (a)	0.0	0.0	0.079	0.079	0.0	0.0
Pamphiliidae (a)	0.533	0.53	0.0	0.0	0.0	0.0
Cimbicidae (a)	0.0	0.0	0.0	0.0	0.609	0.61
Tenthredinidae (a)	0.0	0.0	0.0	0.0	0.382	0.38
Megaspilidae (a)	0.0	0.0	0.172	0.14	0.0	0.0
Ceraphronidae (a)	0.0	0.0	0.222	0.13	0.0	0.0
Braconidae (a)	0.408	0.41	1.24	0.58	0.763	0.76
Ichneumonidae (a)	0.0	0.0	0.201	0.18	0.0	0.0
Mymaridae (a)	0.0	0.0	0.0763	0.040	0.0	0.0
Eulophidae (a)	0.0	0.0	0.102	0.074	0.0	0.0
Encyrtidae (a)	0.0	0.0	0.238	0.14	0.0	0.0
Eupelmidae (a)	0.0	0.0	0.179	0.13	0.0	0.0
Torymidae (a)	0.0	0.0	0.0647	0.044	0.0	0.0
Pteromalidae (a)	0.669	0.40	0.667	0.42	2.21	1.5
Perilampidae (a)	0.0	0.0	0.144	0.090	0.991	0.23
Eucoilidae (a)	0.0	0.0	0.117	0.12	3.05	3.1

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Cynipidae (a)	0.0	0.0	0.287	0.24	1.60	0.84
Proctotrupidae (a)	0.0	0.0	0.0293	0.029	0.0	0.0
Diapriidae (a)	0.533	0.53	0.119	0.067	0.0	0.0
Scelionidae (a)	0.0	0.0	0.409	0.25	0.0	0.0
Platygastridae (a)	1.07	1.1	0.473	0.19	2.14	0.92
Embolemidae (a)	0.0	0.0	0.153	0.13	0.0	0.0
Pemphredonidae (a)	0.136	0.14	0.0	0.0	0.0	0.0
Apidae (a)	0.0	0.0	0.0	0.0	0.382	0.38
Formicidae (a)	2.68	1.6	2.96	1.2	14.3	0.93
Trichoptera	4.55	2.9	3.40	1.6	8.77	2.7
Hydropsychidae (l)	0.669	0.40	0.554	0.30	0.0	0.0
Polycentropodidae (l)	0.669	0.40	0.770	0.64	4.65	2.2
Polycentropodidae (a)	0.136	0.14	0.0	0.0	0.382	0.38
Philopotamidae (l)	0.0	0.0	0.0293	0.029	0.0	0.0
Hydroptilidae (l)	0.0	0.0	0.0	0.0	0.382	0.38
Hydroptilidae (a)	1.60	1.60	0.153	0.088	0.0	0.0
Rhyacophilidae (l)	0.272	0.27	0.477	0.32	0.0	0.0
Limnephilidae (l)	0.0	0.0	0.0616	0.062	1.22	1.2

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Lepidostomatidae (l)	1.20	0.93	1.17	0.39	2.14	0.92
Leptoceridae (l)	0.0	0.0	0.192	0.14	0.0	0.0
Lepidoptera	0.0	0.0	0.0293	0.029	0.382	0.38
Coleophoridae (a)	0.0	0.0	0.0293	0.029	0.0	0.0
Gelechiidae (a)	0.0	0.0	0.0	0.0	0.382	0.38
Diptera	71.1	52	87.9	25	264	171
Tipulidae (l)	0.0	0.0	0.0308	0.031	0.0	0.0
Tipulidae (a)	0.0	0.0	0.0	0.0	0.382	0.38
Psychodidae (a)	0.0	0.0	0.109	0.082	0.609	0.61
Ceratopogonidae (p)	0.533	0.53	0.0	0.0	0.0	0.0
Ceratopogonidae (a)	0.533	0.53	3.05	1.3	0.609	0.61
Chironomidae (l)	16.3	10	9.12	3.0	31.6	9.6
Chironomidae (p)	9.51	5.4	6.79	2.0	20.1	5.6
Chironomidae (a)	15.5	11	52.7	22	161	145
Culicidae (a)	0.0	0.0	0.0293	0.029	0.0	0.0
Simuliidae (l)	27.1	24	5.07	2.3	9.14	9.1
Simuliidae (a)	0.136	0.14	0.166	0.090	0.609	0.61
Deuterophlebiidae (a)	0.0	0.0	0.0587	0.059	0.0	0.0

	Falling		**Reference**		**Rising**	
	Mean	SE	Mean	SE	Mean	SE
Bibionidae (a)	0.0	0.0	0.142	0.12	0.0	0.0
Cecidomyiidae (a)	0.533	0.53	0.711	0.30	1.37	0.15
Mycetophilidae (a)	0.0	0.0	0.116	0.067	2.44	2.4
Scatopsidae (a)	0.0	0.0	0.0792	0.079	1.14	1.1
Sciaridae (a)	0.544	0.54	2.24	0.71	9.91	2.3
Bombyliidae (a)	0.0	0.0	0.0354	0.035	0.0	0.0
Empididae (l)	0.0	0.0	0.0308	0.031	0.0	0.0
Empididae (a)	0.0	0.0	1.32	0.83	1.14	1.1
Phoridae (a)	0.0	0.0	0.177	0.12	0.0	0.0
Anthomyiidae (a)	0.136	0.14	0.0	0.0	0.0	0.0
Muscidae (a)	0.0	0.0	0.0	0.0	0.609	0.61
Sphaeroceridae (a)	0.0	0.0	0.329	0.23	3.20	1.7
Drosophilidae (a)	0.0	0.0	0.0621	0.062	0.0	0.0
Ephydridae (a)	0.272	0.27	5.35	2.7	19.2	16
Unknown larvae	0.0	0.0	0.219	0.18	0.382	0.38
Unknown adult	0.0	0.0	0.0	0.0	0.382	0.38
Araneae	1.48	0.66	2.91	1.4	3.43	3.4
Araneidae (a)	0.533	0.53	0.113	0.089	0.0	0.0

	Falling		Reference		Rising	
	Mean	SE	Mean	SE	Mean	SE
Linyphiidae (a)	0.669	0.40	2.30	1.3	3.43	3.4
Cybaeidae (a)	0.0	0.0	0.0308	0.031	0.0	0.0
Lycosidae (a)	0.136	0.14	0.0	0.0	0.0	0.0
Gnaphosidae (a)	0.0	0.0	0.0223	0.022	0.0	0.0
Thomisidae (a)	0.0	0.0	0.113	0.089	0.0	0.0
Salticidae (a)	0.136	0.14	0.334	0.30	0.0	0.0
Acari	4.28	3.2	2.06	1.4	1.22	1.2
Limnesiidae (a)	4.28	3.2	1.97	1.4	0.609	0.61
Caeculidae (a)	0.0	0.0	0.0247	0.025	0.0	0.0
Oribatei (a)	0.0	0.0	0.0621	0.062	0.0	0.0
Unknown larva	0.0	0.0	0.0	0.0	0.609	0.61
Nematomorpha (a)	0.0	0.0	0.0621	0.062	0.0	0.0
Oligochaeta (a)	0.0	0.0	0.0792	0.079	0.0	0.0

Pond

Most physical and vegetation metrics differed significantly across the study period (Table 18). Water temperature almost doubled between April and July, and there were small but significant differences in pH, conductivity, and total dissolved solids. Canopy height doubled through the season, and percent green cover increased by a factor of ten. In turn, percent senescent ("brown") and litter cover fell through the summer (Table 18). Common tule, *Scirpus acutus*, and the sedge *Carex vesicaria* together dominated the sampled vegetation, accounting for 73% and 25% of cover, respectively.

The pond supports an abundance of macroinvertebrates, and we identified 7,306 organisms representing 13 orders and 26 families. Mean abundances approached 1,000 individuals/m^2, and there were ~20 species/0.56 m^2 (Table 19). There were comparatively few significant differences in faunal metrics at the assemblage level as a function of season, although the higher PIE and lower dominance values for July suggest somewhat higher diversity at that time. The percentage of predators was >70% across seasons (Table 19). All three rank-abundance curves fall between the geometric and log normal models (Fig. 23), indicating relatively high dominance. The curve for July is somewhat divergent from those for April and May and indicates greater evenness among the most abundant taxa but also fewer taxa collected across all samples.

The most abundant orders were Odonata, Diptera, and Coleoptera (Table 20). At the family level, the assemblage was dominated by lestid damselflies, chaoborid and

Table 18. Means and standard errors for physical and vegetation parameters from the Poopenaut pond with results of 1x3 ANOVAs and t-tests. T-tests were only performed when there was a significant ANOVA result. Identical superscripts for a pair of means indicates the lack of a significant t-test difference. TDS= total dissolved solids. * and ** flag differences that were significant at p< 0.05 and p< 0.01, respectively.

	April		**May**		**July**		
Metric	Mean	SE	Mean	SE	Mean	SE	ANOVA
Water depth (cm)	47.5	7.69	68.3	9.85	67.2	1.63	0.12
Water temperature (°C)	12.8	0.339	16.1	0.40	23.8	.200	<0.00001**
pH	6.81^{1}	0.005	6.66^{1,2}		6.40^{2}	.010	0.0015*
Conductivity (μS/cm)	47.0^{1}	1.00	52.0^{1,2}		29.0^{2}	3.00	0.040*
TDS (ppm)	23.5^{1}	0.500	26.0^{1,2}		14.5^{2}	1.50	0.040*
Canopy height (cm)	53.7^{1}	12.0	70.9^{1}	10.1	127	21.4	0.014*
Litter depth (cm)	20.5	5.18	21.0	2.92	20.2	2.47	0.99
Percent bare	0	0	0	0	0	0	NA
Percent green	6.60^{1}	2.09	1.80^{1}	0.20	68.8	2.33	<0.00001**
Percent brown	10.4	3.26	3.60^{1}	0.40	2.20^{1}	1.96	0.048*
Percent litter	83.0^{1}	5.19	56.6^{1,2}	15.8	29.0^{2}	3.32	0.0074**
Percent tree shading	4.99	3.47	17.5	17.5	1.25	0.764	0.52

Table 19. Means and standard errors for assemblage metrics from the Poopenaut pond with results of 1x3 ANOVAs and t-tests. T-tests were only performed when there was a significant ANOVA result. Identical superscripts for a pair of means indicates the lack of a significant t-test difference. Richness metrics and PIE are scaled to 0.75 m^2. * and ** flag differences that were significant at $p < 0.05$ and $p < 0.01$, respectively.

	April		**May**		**July**		
Metric	Mean	SE	Mean	SE	Mean	SE	ANOVA
Total individuals/m^2	924	119	755	58.3	930	62.6	0.29
Family richness	13.0	0.447	13.8	0.583	13.4	0.812	0.68
Species richness	19.8	1.07	21.0	0.949	19.0	0.775	0.35
Expected no. of families	11.1	0.397	12.4	0.626	11.9	0.651	0.32
Expected no. of species	16.2	1.18	17.6	1.12	16.9	0.581	0.62
PIE	0.698^1	0.0399	0.657^1	.0415	0.794	0.0218	0.049*
% Family dominance	51.3^1	4.63	53.0^1	4.95	36.5	3.75	0.045*
% Species dominance	51.3^1	4.63	53.0^1	4.95	36.5	3.75	0.045*
% Predators	79.8	4.94	70.4	3.32	76.1	3.38	0.28

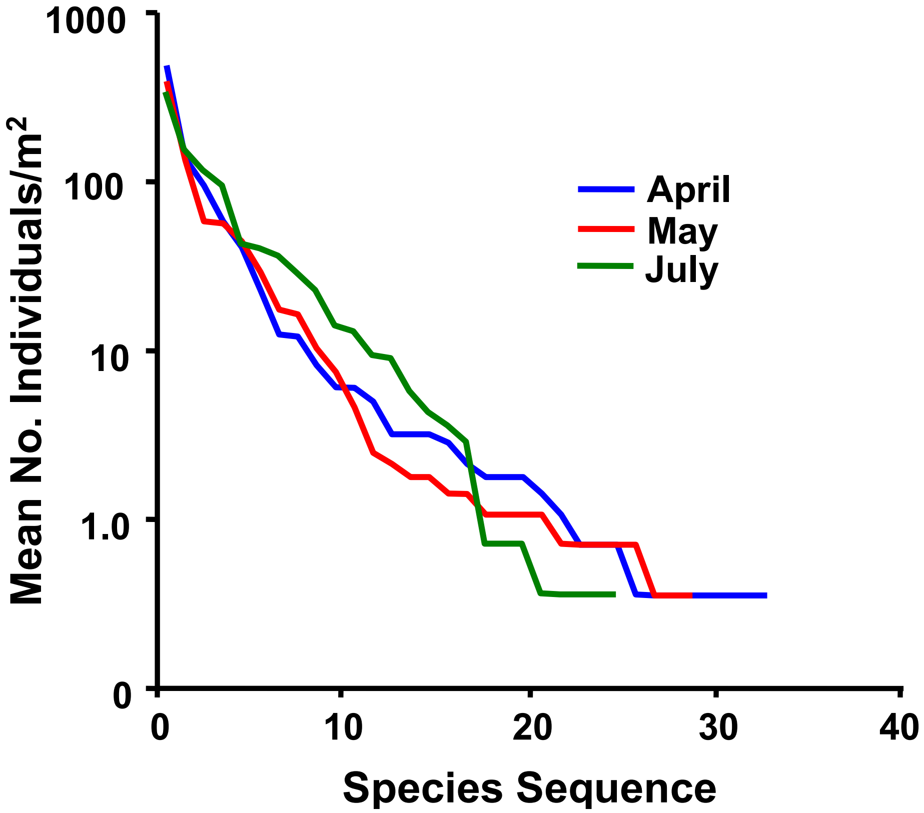

Fig. 23. Rank-abundance plots for pond assemblage showing seasonal trends (log scale).

chironomid midges, dytiscid diving beetles, and libellulid dragonflies. All of these families are predaceous except Chironomidae.

In contrast to the lack of seasonal differences at the assemblage level, most order and family populations differed significantly across months (Table 20). Further, most fauna demonstrated progressive population change throughout the summer, but these seasonal trends were in two distinct directions. Libellulids, lestids, hydrophilid water scavenger beetles, culicid mosquitos, and ostracods were all most abundant in early season, whereas ephemeropterans, aeschnid dragonflies, corixid water boatmen, notonectid backswimmers, chaoborids, chironomids, and clams were all most abundant in late season (Table 20).

Discussion

Assemblage Structure

We collected a diverse assemblage of macroinvertebrates that was generally similar to the assemblage in the riffle habitats in the upper Merced River that were at approximately the same elevation and that had similar ecological characteristics (Stillwater Sciences 2007). Many of the families were common to both studies, including all mayfly families. Each stream had one beetle, one fly, and one stonefly that the other stream lacked. The Merced River had four caddisfly families that were absent from the Tuolumne River, and the Tuolumne River had three caddisfly families that were absent from the Merced River. The upper Merced River comparison sites had four families of mites that we did not find in the upper Tuolumne River, but the upper Tuolumne River had one mite family that was absent from the Merced as well as

Table 20. Per m^2 means and standard errors for Poopenaut pond populations with resullts of 1x3 ANOVAs and t-tests. ANOVAs were only performed for orders and families, and t-tests were only performed for orders. Further, t-tests were only performed when there was a significant ANOVA result. Identical superscripts for a pair of means indicates the lack of a significant t-test difference. * and ** flag differences that were significant at $p < 0.05$ and $p < 0.01$, respectively. n= nymph, l= larva, p= pupa, a= adult, v= various size classes.

	April		**May**		**July**		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Collembola	1.42	1.0	1.42	1.0	0.356	0.36	0.62
Sminthuridae	1.42	1.0	1.42	1.0	0.356	0.36	0.62
Sminthurus eiseni (a)	1.42	1.0	1.42	1.0	0.356	0.36	
Ephemeroptera	0.0^1	0.0	0.0^1	0.0	22.4	5.1	0.00016**
Baetidae	0.0	0.0	0.0	0.0	22.4	5.1	0.00016**
Callibaetis sp. (n)	0.0	0.0	0.0	0.0	22.4	5.1	
Odonata	624	104	450	35	166	29	0.0012**
Aeschnidae	0.0	0.0	0.0	0.0	4.62	3.0	0.13
Aeschna sp. (n)	0.0	0.0	0.0	0.0	4.27	2.7	
Anax walsinghami (n)	0.0	0.0	0.0	0.0	0.356	0.36	
Libellulidae	137	34	56.5	17	8.89	3.2	0.0045**
Sympetrum sp. (n)	137	34	56.5	17	8.89	3.2	

	April		May		July		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Lestidae	487	82	393	37	152	31	0.003**
Lestes stultus (n)	487	82	393	37	152	31	
Hemiptera	5.69[1]	3.1	8.53[1]	5.1	55.1	9.7	0.00026**
Gerridae (n)	0.356	0.36	1.07	0.44	0.711	0.44	0.49
Corixidae	4.98	2.8	7.47	5.0	35.9	7.7	0.0031**
Corisella sp. (n)	4.98	2.8	7.47	5.0	2.13	1.0	
Corisella sp. (a)	4.98	2.8	7.47	5.0	33.8	6.7	
Notonectidae	0.356	0.36	0.0	0.0	18.5	2.7	<0.00001**
Buenoa sp. (n)	0.0	0.0	0.0	0.0	2.13	1.0	
Buenoa sp. (a)	0.0	0.0	0.0	0.0	3.56	1.5	
Notonecta sp. (n)	0.356	0.36	0.0	0.0	9.25	2.8	
Notonecta sp. (a)	0.0	0.0	0.0	0.0	3.56	1.5	
Coleoptera	120	38	45.9	17	120	29	0.16
Gyrinidae	1.78	1.4	0.0	0.0	0.711	0.44	0.35
Gyrinus sp. (l)	0.711	0.44	0.0	0.0	0.711	0.44	
Gyrinus sp. (a)	1.07	1.1	0.0	0.0	0.0	0.0	
Dytiscidae	108	38	42.0	17	119	29	0.17
Agabus sp. (l)	1.78	1.4	0.356	0.36	0.0	0.0	

	April		May		July		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Desmopachria sp. (a)	94.6	35	29.2	11	3.56	1.6	
Dytiscus sp. (l)	0.356	0.36	0.356	0.36	0.0	0.0	
Hydroporus sp. (l)	8.18	2.6	10.3	6.0	116	29	
Laccornis sp. (a)	0.356	0.36	0.0	0.0	0.0	0.0	
Liodessus sp. (a)	2.84	2.1	1.78	1.4	0.0	0.0	
Hydrophilidae	9.60	3.3	3.91	0.36	0.356	0.36	0.016*
Berosus fraternus (l)	0.0	0.0	0.711	0.44	0.356	0.36	
B. fraternus (a)	6.05	3.5	0.356	0.36	0.0	0.0	
Enochrus sp. (l)	1.07	0.71	1.42	0.87	0.0	0.0	
Enochrus sp. (a)	0.711	0.71	0.0	0.0	0.0	0.0	
Hydrochus sp. (l)	0.711	0.71	0.711	0.44	0.0	0.0	
Hydrochus sp. (a)	0.356	0.36	0.0	0.0	0.0	0.0	
Tropisternus sp. (l)	0.711	0.44	0.711	0.44	0.0	0.0	
Diptera	130[1]	28	87.8[1]	26	507	60	0.000017**
Ceratopogonidae	3.20	1.7	4.62	2.7	0.0	0.0	0.30
Bezzia/Palpomyia (l)	3.20	1.7	2.13	1.4	0.0	0.0	
Bezzia/Palpomyia (p)	0.0	0.0	2.49	2.1	0.0	0.0	

	April		**May**		**July**		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Chaoboridae	12.1	4.1	16.4	5.1	334	35	<0.00001**
Chaoborus sp. (l)	12.1	4.1	14.9	4.5	287	30	
Chaoborus sp. (p)	0.0	0.0	1.42	1.0	46.9	17	
Culicidae	50.9	21	1.42	0.67	0.0	0.0	0.017*
Ochlerotatus sticticus (l)	3.20	1.4	0.0	0.0	0.0	0.0	
Ochlerotatus sp. (p)	40.9	19	0.711	0.44	0.0	0.0	
Culex sp. (l)	0.711	0.71	0.711	0.71	0.0	0.0	
Aedes/Ochlerotatus (l)	0.711	0.71	0.0	0.0	0.0	0.0	
Aedes/Ochlerotatus (p)	5.33	5.3	0.0	0.0	0.0	0.0	
Chironomidae	63.7	19	65.4	23	174	29	0.0098**
Chironomini (l)	1.78	1.8	2.49	2.5	8.89	2.8	
Chironomini (p)	0.356	0.36	0.0	0.0	0.356	0.36	
Orthocladiinae (l)	51.6	16	54.8	23	41.3	10	
Orthocladiinae (p)	6.76	2.1	3.20	1.6	1.07	0.71	
Tanypodinae (l)	0.0	0.0	0.356	0.36	27.4	3.6	
Tanypodinae (p)	0.0	0.0	0.356	0.36	1.07	0.44	
Tanytarsini (l)	3.20	2.1	4.27	1.7	90.7	19	
Tanytarsini (p)	0.0	0.0	0.0	0.0	3.20	1.2	

	April		**May**		**July**		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Acari	1.07[1]	0.44	3.56	1.3	0.356[1]	0.36	0.035*
Hydrachnidae	0.711	0.44	0.0	0.0	0.356	0.36	0.33
Hydrachna sp. (a)	0.711	0.44	0.0	0.0	0.356	0.36	
Limnocharidae	0.356	0.36	2.13	0.87	0.0	0.0	0.036*
Limnochares sp. (a)	0.356	0.36	2.13	0.87	0.0	0.0	
Pionidae	0.0	0.0	0.356	0.36	0.0	0.0	0.40
Huitfeldtia sp. (a)	0.0	0.0	0.356	0.36	0.0	0.0	
Arrenuridae (a)	0.0	0.0	1.07	1.1	0.0	0.0	0.40
Laevicaudata	12.5	6.6	17.4	4.4	2.85	1.1	0.12
Lynceidae	12.5	6.6	17.4	4.4	2.85	1.1	0.12
Lynceus brachyurus (v)	12.5	6.6	17.4	4.4	2.85	1.1	
Cladocera	22.8[1]	14	134	29	39.8[1]	18	0.0065**
Daphnidae	22.8	14	134	29	39.8	18	0.0065**
Ceriodaphnia sp. (v)	22.8	14	134	29	39.8	18	
Ostracoda (v)	5.69[1]	1.7	2.85[1]	0.91	0.356	0.36	0.021*
Hirudinea	0.356	0.36	0.0	0.0	0.0	0.0	0.40
Glossiphoniidae	0.356	0.36	0.0	0.0	0.0	0.0	0.40
Helobdella elongata (v)	0.356	0.36	0.0	0.0	0.0	0.0	

	April		May		July		
	Mean	SE	Mean	SE	Mean	SE	ANOVA
Gastropoda	0.711	0.44	2.85	1.1	1.07	0.44	0.12
Limnaeidae (v)	0.0	0.0	0.0	0.0	0.356	0.36	
Planorbidae	0.711	0.44	2.85	1.1	1.07	0.44	0.12
Gyraulus deflectus (v)	0.356	0.36	1.78	0.56	0.0	0.0	
Helisoma sp. (v)	0.356	0.36	0.0	0.0	0.711	0.44	
Planorbella sp. (v)	0.0	0.0	1.07	0.71	0.0	0.0	
Bivalvia	0.0[1]	0.0	0.0[1]	0.0	13.9	6.5	0.035*
Sphaeriidae	0.0	0.0	0.0	0.0	13.9	6.5	0.035*
Sphaerium sp. (v)	0.0	0.0	0.0	0.0	13.9	6.5	

bivalves. Sorensen's similarity coefficient was 0.68 for families and 0.59 for species. Like Stillwater Sciences (2007), we did not collect any New Zealand mudsnails, and it is likely that Yosemite National Park is free of these exotics at this time.

By way of further comparison, the reach of the upper San Joaquin River in Devils Postpile National Monument is a nearby river at about twice the elevation of the Poopenaut Valley (2300 versus 1100m) but with a fauna (Holmquist and Schmidt-Gengenbach 2005) that was not much more different from the upper Tuolumne than the upper Merced, despite the difference in elevation. Most of the families collected were shared by both the upper San Joaquin and upper Tuolumne. Although both streams again had the same families of mayflies, there were four families of caddisflies that were found in the Poopenaut Valley that were not found in the Postpile, and vice versa. There were three families of Plecoptera and one dipteran and one hemipteran family that were found in the Postpile but not in the Poopenaut, but dobsonflies, bivalves, and one family of beetle were found in the Poopenaut but not in the Postpile. Sorensen's similarity coefficient was 0.68 for families, i.e., exactly the same as for the Tuolumne-Merced comparison, and species similarity (0.53) was only slightly lower than the Tuolumne-Merced similarity (0.59).

Rank-abundance plots retain much more information than diversity indices that, used alone, distill complex communities into single numbers with accompanying information loss, and rank-abundance plots are therefore useful components of initial assemblage descriptions (Stiling 2001, Magurran 2004, Underwood and Fisher 2006. The family and species rank abundance plots (log scale; Figs. 9,11) fall between the log normal distribution and MacArthur's broken stick model. These curves indicate relatively high richness and evenness, minimal niche preemption, and relatively uniform division of resources (Magurran 2004, Schowalter 2006).

Collector-gatherers dominated the functional feeding groups at 70.9% of individuals and 31.8% of taxa. Collector-gatherers in combination with collector-filterers accounted for 84.4% of individuals, which exceeds the high 70% found in the upper Merced (Stillwater Sciences 2007). Such a high proportion of collector-gatherers, or a low collector-filterer:collector-gatherer ratio (which also occurred in the Poopenaut reach at 0.19), can suggest a relatively low ratio of suspended fine particulate matter to deposited fine particulate matter (Merritt and Cummins 1996, Merritt et al. 2008), which in turn can be related to reduction in transported particulates below deep release dams (Allan 1995). Predatory taxa accounted for 44.6% of species, but only 7.5% of individuals. The ratio of predators to all other feeding groups (0.75) was somewhat lower than the frequently encountered range of 0.10-0.20 (Merritt and Cummins 1996, Merritt et al. 2008). Scrapers were less important in our upper Tuolumne samples (2%) than in the upper Merced (21%; Stillwater Sciences 2007).

It is encouraging that there were so few tolerant fauna (see Methods) in the riffles below the dam. Our one tolerant taxon, the clam *Sphaerium*, accounted for only 1.4% of taxa and 0.26% of individuals. In contrast, tolerant taxa represented 14% of taxa in the riffles in the upper Merced. Hilsenhoff's Biotic Index (HBI), which weights tolerance by abundance, was relatively low at 4.01 across our samples. Percent Ephemeroptera-Plecoptera-Trichoptera (EPT) was in turn high at 78.8% of total individuals and 64% of taxa.

Although the detection of seasonal patterns was not a goal of this study, some patterns emerged, particularly when comparing spring-summer months with fall-winter months. There were significant increases in Diptera, collector-filterers, and HBI and a concomitant decrease in %EPT, in large part due to an increase in *Simulium* black flies. Somewhat surprisingly, there was also a decrease in Percent Species Dominance, which was largely a function of increased richness and abundance of Chironomidae (Diptera) during the fall and winter. Benthic invertebrate sampling is often done in the summer and/or fall, but clearly year-round sampling is desirable when possible because of the shifting nature of the assemblage.

The ancillary sampling of boulders and slabs indicated that these habitats have twice the faunal density of riffles in this reach, but also that this density is highly variable. These large rock substrata had a strikingly different assemblage structure than the riffles in some cases. For example the mean of 276 elmid beetles/m^2 was 64 times greater than the mean for riffles.

Habitat assessments indicated that in general this river reach should provide good habitat for fauna (overall score of 155 was at the low end of the Optimal range; Table 3). The mean habitat quality score fell into the lower range of scores for the nearby upper Merced River (Stillwater Sciences 2007). RMC Water & Environment and McBain & Trush (2006) identify reduction of magnitude and duration of snowmelt flows and reduced winter peak flood magnitude as likely consequences of flow regulation below the O'Shaughnessy Dam with potential effects on geomorphology, riparian vegetation, and fauna (see also Chapter 2 of this report). Reduced flow variability can lead to reduced habitat heterogeneity and increased algal cover and sediment deposition (Allan 1995). Carter and Fend (2001) found several of these factors to be important in structuring the BMI assemblage in the upper Merced. There was a lack of woody debris at our sites, and there was generally a substantial cover of filamentous green algae (Figs 2-4). There were, however, plentiful green algae in the river above the reservoir as well (pers. obs.). There was clear evidence of sediment deposition at some sites, though the mean for this parameter fell just within the Optimal range, and this parameter was a significant predictor of baetid mayfly abundance at our sites.

Stream width, depth, and flow in the study reach of the Tuolumne River (Table 2) were generally similar in riffle habitats in the upper Merced River (Stillwater Sciences 2007). Temperatures from the Poopenaut reach of the Tuolumne, however, appear to have been substantially lower than those from the upper Merced: 7.81 ^{o}C (mean from our 2007 September and October samples) versus 13.3 ^{o}C (our calculated mean for the upper Merced based on fall 2006 data in Stillwater Sciences 2007). The much more extensive data from temperature recorders above and below the reservoir and on the upper Merced (Chapter 2) confirm this observation. Hypolimnial releases from dams typically reduce daily and annual temperature fluctuations and lower mean summer temperatures (Ward and Stanford 1979) and raise mean winter temperatures (RMC Water and Environment, McBain and Trush 2006). These changes often lead to negative impacts on BMI diversity because of disruption and/or damping of thermal cues for reproduction and development, reduction of degree days for completion of life cycles, and slowing of metabolic rates, particularly during summer (Hayden and Clifford 1974, Lemkuhl 1974, Allan 1995), and Hawkins et al. (1997) found temperature to be a key factor in structuring BMI. RMC Water & Environment and McBain & Trush (2006) note that fauna are likely to be similarly affected by disrupted thermal regimes below the O'Shaughnessy Dam. Although diversity is often reduced in response to increased temperatures, overall production can be increased (Wohl et al. 2007). Summer water temperatures below the dam are clearly lower than above-reservoir and Merced River temperatures (Chapter 2 in this report), but our first year of study did not include an above-reservoir comparison group, precluding conclusions about temperature regime and the influence of the dam and reservoir on downstream BMI along this isolated reach. We did not find increases in BMI diversity or decreases in tolerance with increasing distance downstream from the dam, suggesting that temperature effects *may* not be as pronounced as seen below some other cold-water dams (Ward and Stanford 1979, Allan 1995). The 5 km study reach, however, may have been insufficient in length to have allowed appreciable warming before the discharged water left the study area.

This first year of study was designed to be an initial characterization of the BMI assemblage in riffle habitats that could be used as baseline data. Year-to-year variability can be substantial (Leland et al. 1986, Holmquist and Schmidt-Gengenbach 2005), and we advocate continued monitoring of this reach, including additional habitats, in order to establish a longer-term baseline and to detect effects due to changes in dam operations, climate, and other factors.

The Year 1 assemblage characterization yielded some results suggesting some level of impact due to dam operations, whereas other results provide an initial indication of little if any negative effect, but this first year of study was not designed to be an assessment of effects of stream regulation. Comparison of below-dam, above-reservoir, and unregulated reaches can be a powerful tool to discriminate potential effects of dam operations, with the caveat that these reaches can also differ as a function of geomorphological or other covariates (Holmquist et al. 1998, Greathouse et al. 2006a,b). Multi-year comparisons of this nature would be an important complement to the ongoing Looking Downstream efforts.

Response to Experimental Releases

The 2008 and 2009 releases were very different, and although these differences make the two releases imperfect replicates, the two releases capture many different variables and influences on the benthic macroinvertebrate assemblage. Before-After assemblage differences in 2008 were clearly attributable to the experimental release, as this release was a one-day event, and we sampled the day before and the day after the release. Confounding seasonal effects were absent. The 2008 release occurred in late May. In contrast the 2009 release started earlier, in late April, and ended later, in mid July. This longer release much more closely approximated a natural spring pulse, but was also long enough that seasonal dynamics in the invertebrate assemblage, apparent from our year long 2007-2088 sampling, likely overlie results attributable to release effects. Further, the After-Two-Months sampling occurred in September of 2009, versus July of 2008, so the last 2009 sampling interval was almost certainly affected by seasonal dynamics as well. Such a seasonal overlay is likely to be particularly significant in an area such as Hetch Hetchy with strong seasonality, particularly in the temperature regime. The long duration of the falling hydrographic limb probably allowed recovery of populations during the period in which flows were low enough that scour was reduced but still high enough to preclude sampling. Thus, three of the five most important hydrological factors that regulate the ecology of streams (magnitude, frequency, duration, timing, and rate of change of flow; Richter et al. 1996, Poff et al. 1997, Cortes et al. 1998) differed between the two years; magnitude and frequency of flooding was similar in 2008 and 2009. In addition, the 2008 release was likely to have created some persisting effects that carried over to the 2009 pre-release assemblage, i.e., some populations may not have recovered in the ensuing year. Lastly, it appeared that in 2009 there was more sand and silt deposited in slower sections of riffles just downstream of catchments than was present in 2008. The increased presence of fines in 2009 may have been an important influence on some taxa. These many differences between the two releases probably account for many of the divergent invertebrate changes associated with the 2008 and 2009 releases. The two releases were good complements: effects of the 2008 release were more easily interpreted, whereas the 2009 release more closely replicated a natural spring flood (Chapter 2).

The 2008 release had major immediate effects on BMI and algae, and some of these effects would be generally viewed as positive changes to the BMI assemblage. Total abundance and all order abundances fell in 2008, but dominance decreased and evenness increased. Robinson et al. (2003) observed similar shifts in an assemblage following a series of experimental releases. Losses of Chironomidae were striking, perhaps because of a known proclivity for drift, i.e., leaving the substrate either actively or passively to enter the water column, as a response to floods (Perry and Perry 1986, Wallace 1990, Imbert and Perry 2000, Jakob et al. 2003) and perhaps also due to association with filamentous green algae, much of which was apparently removed by the 2008 release. Proportions of taxa indicative of lotic system health increased, e.g. Ephemeroptera-Plecoptera-Trichoptera, predators, and intolerant taxa as indicated by Hilsenhoff's Biotic Index. Jakob et al. (2003) found no significant response of Ephemeroptera and Plecoptera to a series of experimental releases and attributed the lack of response to morphological and behavioral adaptations to torrential flow (see also Holomuzki and Biggs 2000). Although %EPT increased in our study, there *were* losses of all of these taxa in response to the release—but at a lower rate than was found for other groups. There were significant but mixed effects on richness measures in our Tuolumne system; effects on richness were generally negative. Overall declines in macroinvertebrate abundance and richness have also been noted in response to similar release experiments (Jakob et al. 2003, Robinson et al. 2003).

Assemblage dynamics were different in 2009, probably due in large part to the later post-release sampling and recovery of some populations during the falling hydrographic limb. Total individuals decreased only minimally after the release and increased dramatically by two months after the release. Abundances of all orders except Diptera did fall in response to the 2009 release, as in 2008, but dominance increased instead of decreasing. This opposite response was proximately due to the slight increase in Diptera and probably ultimately due to late summer increases in chironomids and simuliids which were apparently sufficient to compensate for losses due to scour and active drift. Actual increases in simuliids may have been even greater than our results suggest, because simuliids can be difficult to dislodge by kick netting (Armitage 1976). Proportion of EPT decreased, instead of increasing as in 2008, probably for the same reasons. As in 2008, there was a general downward trend for richness and diversity metrics after the release.

Green algal biomass was greatly reduced in 2008, and such reductions have been found in association with other experimental releases (Jakob et al. 2003). Algal reductions in response to releases have been found to be less severe close to dams (Jakob et al. 2003) as a result of lack of scouring material (Shannon et al. 2001). In our study, there were not longitudinal differences along the studied river reach, despite our study reach being longer in length than that used by Jakob et al. (2003). Pre-release algal biomass in 2009 was half that of pre-release 2008, possibly due to lack of recovery from the previous year, though green algae grows quickly and proliferates in the constant low flow often found below dams, (Cortes et al. 1998). There were no net algal losses associated with the 2009 release, probably because of recovery from the initial scouring during the long falling hydrographic limb, i.e., there was likely extensive regrowth during the extended time required for the river to drop to a level that could be sampled after the release.

The food web was clearly modified by the 2008 release. The proportion of collector-gatherers was reduced by the release in the short term, and the collector-filterer:collector-gatherer ratio increased from a very low 0.0077 to 0.068 immediately after the release. More importantly, this ratio was still higher than pre-release levels two months later (0.058). The persistence of the increase in collector-filterers may have been the result of an increased ratio of suspended fine particulate matter to deposited fine particulate matter (Merritt and Cummins 1996, Merritt et al. 2008). Such a shift in this particulate ratio was probably not a result of increased suspended particulates over the two month period after the release, unlikely below a deep release dam (Allan 1995), but was more likely a result of removal of deposited fines (Eustis and Hillen 1954, Johnson et al. 1995, Henson et al. 2007) by the release. Silt deposition favors many collector-gatherers, for instance Tanytarsini (Chironomidae; Armitage 1976). Although suspended particulates likely only increased during and immediately after the release (Jakob et al. 2003), reduction of these particulates is common below dams without surface discharge (Allan 1995). Much of this material is allochthonous in nature, and dams can disrupt the hydrological connectivity with upstream reaches and uplands (Allan 1995, Pringle 2006). In 2009, the collector:filterer ratio was initially low (0.023) and remained so (0.013) immediately after the release, but rose to a very high 0.42 two months after the release due to the rapid increase in simuliids in the early fall. Prior to the 2008 release, the proportion of predators (0.030; Table 11) was lower than in our 2007-8 baseline sampling (0.075; Table 6), which in turn was lower than the more frequently encountered range of 0.10-0.20 (Merritt and Cummins 1996, Merritt et al. 2008). Immediately after the release, the proportion of predators rose into the 0.10-0.20 range (0.12) but fell again by two months after the release (0.037). In 2009, the proportion of predators was 0.11, but this proportion was reduced by about two-thirds after the release and stayed at approximately that level into the fall. The proportion of predators was apparently lowered by the large number of baetids, chironomids, and simuliids.

Many of the apparent responses to the releases lessened in the months immediately following the releases, as has been found in analogous studies (Jakob et al. 2003, Robinson et al. 2003). This response was particularly notable in 2008 but was present in 2009 as well. After two months many metrics had levels between those observed immediately before and immediately after the release. Chironomids recovered much of their abundance in the two months following the release (greatly exceeding initial abundances in 2008), and we observed increases in Baetidae and Simuliidae as was also observed by Robinson et al. (2003), although we did not observe the broad increase in Plecoptera that these authors recorded. All three of these groups have adaptations that allow rapid colonization of denuded substrata (Robinson and Minshall 1986, Robinson et al. 2003). It is encouraging that some of the positive effects of the release persisted for at least two months; much of this change is likely due to provision of bare substrata lacking sediment and algal cover (Ward 1976, 1984). The releases were valuable experiments that provided a first indication of how river health might respond to an intact disturbance regime.

Although some effects of the releases may be transitory, others are likely to persist for some time. Both periphyton and sediments are mobilized rapidly by artificial releases (Jakob et al. 2003). But, as algae recolonize substrata, faunal metrics related to algal growth (Armitage 1976) would be expected to return over a period of months to levels seen before the release. In contrast, faunal metrics driven by sedimentation would be expected to remain changed for years, because sediment would take some time to reaccumulate to pre-release levels (Ward 1984).

In general, river health will benefit from river regulation that mimics the natural pattern of flooding as closely as possible (Morehardt 1986, Bayley 1991, Jobin 1998), in part because spring flooding is a key natural disturbance (Resh et al. 1988, Townsend et al. 1997, Vinson 2001). Robinson et al. (2003) caution that responses to new release programs continue to develop over a period of years, rather than months, as the assemblage adjusts to a new and more variable habitat configuration. These authors argue that release programs and associated benthic sampling should be sustained if managers desire a more natural macroinvertebrate assemblage.

An observational study that includes not only the below-dam reach, but also 1) the above-reservoir reach, and 2) unregulated tributaries to the Tuolumne River that share the same elevation as the Poopenaut reach, would be a key element in developing context for current river condition. It would also be useful to compare the assemblage below Lake Eleanor, which has a different discharge regime, to the assemblage below the Hetch Hetchy reservoir.

Drift response to changing flow

Overall drift densities fell within the typical range of 100-1,000 individuals/100m^3 (Allan 1995), although our numbers were at the lower end of this spectrum, particularly when aquatic densities were considered in isolation. Aquatic phase chironomids often dominate the drift (e.g., Tonkin et al. 2009), and adult chironomids were the most abundant form in our samples, followed by chironomid larvae and pupae. The high densities of chironomids, particularly adults, that were present with rising discharge lowered various measures of diversity for the drift associated with increasing flow.

Both increasing and decreasing discharge resulted in drift densities that were higher than reference densities. Drift of aquatic forms generally increased with decreasing discharge during our study, and this inverse relationship of aquatic drift density and discharge is common (Minshall and Winger 1968, Gore 1977, Canton et al. 1984, Perry and Perry 1986, Poff and Ward 1991, Dewson et al. 2007). Reduction of available habitat and associated benthic density increases are one cause of this phenomenon (Perry and Perry 1986), as is inadequate flow for feeding or physiology (Dewson et al. 2007). Further, predator density may increase as wetted area and depth decrease, and predator avoidance may cause fauna to enter the drift in large numbers (Dewson et al. 2007). Relatively higher drift densities with falling discharges may also be a function of concentration of drift, and in turn there can be dilution of drift with increasing discharge (Perry and Perry 1986). In other instances, aquatic drift density can increase with discharge, likely primarily due to dislodgement during spates (Waters 1972, Scullion and Sinton 1983, Perry and Perry 1986, Poff and Ward 1991, Imbert and Perry 2000, Robinson et al. 2003, Mochizuki et al. 2008). We did not observe overall increases in aquatic drift density with increasing discharge, but terrestrial fauna did have higher drift densities with increasing discharge, probably due to terrestrial fauna becoming trapped by the rising waters. Temperatures decreased during releases due to the influx of cold reservoir water, and this pattern was seen for both examined temporal scales. These temperature changes may represent an additional influence on invertebrate activity and ultimately on drift patterns.

Response to drift differs as a function of taxon and may also differ widely across examined lotic environments. For instance, decreasing discharge in the upper Colorado River increased drift for most taxa, including baetid and heptageniid mayfly taxa and simuliid blackfly larvae but decreased drift of leptophlebiid and ephemerellid mayflies and lepidostomatid caddisfly larvae (Poff and Ward 1991). Perry and Perry (1986) found increasing discharge to increase drift of chironomids and baetids in two Montana rivers. We found baetids to have three to five times greater drift densities in both rising and falling discharge than in reference conditions. We also found heptageniid and simuliid density increases in conjunction with falling discharge. Further, in our study, falling discharge resulted in higher, not lower, leptophlebiid and ephemerellid mayfly densities. Lepidostomatid drift did not decrease with discharge in our samples, as observed by Poff and Ward (1991), but rather increased on both rising and falling discharge; the same held for chironomids. Comparison of the overall drift densities with our 2007-2009 benthic samples indicates that heptageniids occurred in proportionally greater numbers in the drift than in the benthic samples. Conversely, despite relatively high benthic abundance, chironomid larvae and pupae were found in disproportionately low numbers in the drift, as were leptophlebiid nymphs. The relatively low chironomid drift densities are of note, because chironomid abundance in benthic samples was apparently lowered by the 2008, but not the 2009, experimental release. Some of these differences may have been mediated by differences in algal cover, which was particularly high in 2008. Large amounts of filamentous green algae were mobilized by the 2008 event, and chironomids living in the algae may have been removed along with the plant material.

The drift work was an ancillary addition to our 2010 sampling, but this initial effort yielded important information. We now know the basic composition of the below-dam drift and the relative importance of aquatic and terrestrial components. It appears that below-dam decreases or increases in discharge will result in increased drift densities; the former had more influence on aquatic fauna and the latter on terrestrial fauna. This information should be useful in understanding the functional ecology of the river, predicting changes to assemblage structure and tolerance levels as a function of releases, and quantifying food resources for fishes (Waters 1972). Drift is nonetheless a complex phenomenon, and our sampling provides only an initial indication of the factors that structure drift. Drift is influenced by seasonal patterns in population structure and life histories, antecedent conditions at a variety of scales, proximity to dams, substrate, algal cover, predation, depth, portion of the river cross-section examined, rapidity and amplitude of discharge changes, and particularly time of day (Waters 1972, Tonkin et al. 2009). It may be worthwhile to examine the influence of one or more of these variables in the future.

Poopenaut Pond

Although abundance, richness, and diversity of ponds can either increase (Meyer et al. 2011) or decrease (Christensen and Crumpton 2010) with increasing vegetation structure, assemblage metrics in the Poopenaut Pond were similar through the sampling periods, despite large increases in vegetation structure and temperature as well. One suite of fauna exhibited strong decreases through the summer, while another demonstrated commensurate increases. The result was remarkably little change at the assemblage level, despite the striking changes at the population level, underscoring the importance of not relying on one, or a small number of, assemblage metrics in isolation. Bidirectional trends among these taxa are relatively common in ephemeral ponds (Duffy 1999, Holmquist and Schmidt-Gengenbach 2006). Predator abundance, accounting for 70-80% of the assemblage, was particularly high throughout the season, although dominant predators changed over time. Predation pressure tends to be highest in ponds of longer duration (Wiggins et al. 1980, Schneider and Frost 1996, Zedler 2003, Holmquist and Schmidt-Gengenbach 2006) such as the Poopenaut Pond. Mosquitos are often greatly reduced after early season by predation these ponds (Schneider and Frost 1996, Holmquist and Schmidt-Gengenbach 2006), and such was the case in the Poopenaut Pond as well, where mosquito abundance fell from 51/m^2 to zero over three months.

The pond fauna adds considerably to the total biodiversity of the Poopenaut ecosystem. The pond contributed an additional five orders and twenty families to those identified from the river benthos during 2007-2009. Species dominance in the pond was higher than that of the river, but family dominance was similar. In 2010, we allocated a relatively large amount of effort to each of three sampling trips, but we will be likely to add taxa (MacKenzie and Royle 2005, Curtis and Paton 2010), and gain temporal resolution, by doubling the number of sampling trips and allocating somewhat less sampling intensity to each during our planned 2011 sampling. In addition, we will be sampling the small, short-lived ponds on the west side of the river during 2011, and these ponds are likely to add additional taxa, particularly vulnerable, fugitive prey species (Holmquist et al., submitted), that would be unlikely to survive in the large and more persistent Poopenaut Pond.

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