

Interim report
The Tuolumne River below Hetch Hetchy Reservoir: Characterization of the benthic macroinvertebrate assemblage and response to an experimental spring flood event



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Summary

Benthic macroinvertebrates are excellent integrators of physical, chemical, and biological processes and are highly valued as indicators of stream health. During 2007-2008, we characterized the Poopenaut Valley invertebrate assemblage. In spring of 2008, we investigated the response of the assemblage to an experimental spring flood event.

Assemblage Structure

For the 2007-8 assemblage description, we sampled macroinvertebrates in the riffles of the Poopenaut Valley reach at approximately six-week intervals for one year. This sampling produced baseline data on assemblage structure, trophic groups, the level of "tolerance" to degraded conditions exhibited by the fauna (low tolerance generally indicates healthy stream conditions), the physical environment, and overall habitat quality.

We sampled with kick nets as per US Environmental Protection Agency rapid bioassessment protocols and calculated metrics emphasized richness, dominance, trophic roles, and tolerance. Key physical measurements included flow, depth, temperature, and stream width, and we also completed EPA habitat assessments at each site.

We collected 69 taxa representing 25 families and eight orders. Ephemeroptera were found in every sample, and this order was dominated by Baetidae, Ephemerellidae, and Leptophlebiidae. Plecoptera were lower in abundance but were still found in every sample. Trichoptera were similar to Plecoptera in abundance, and

the most common caddisfly families were Hydropsychidae, Hydroptilidae, and Philopotamidae. Coleoptera were relatively uncommon, and Elmidae and Hydrophilidae were the only families collected. Diptera was the most abundant order, and in turn Chironomidae and Simuliidae were the most common dipterans.

The majority of species were either predators or collector-gatherers, but collector-gatherers accounted for 71% of total individuals, whereas predators only represented 7.5% of individuals. Tolerance values ranged from 0 to 8, but there were 36 intolerant taxa and only one intolerant taxon. This one tolerant taxon, a clam, represented 1.4% of taxa and only 0.26% of individuals. Diptera increased three-fold during the fall and winter, and in turn overall tolerance of the assemblage increased from low to moderate levels during this time.

A high proportion of collector-gatherers, or a low collector-filterer:collector-gatherer ratio (which also obtained in the Poopenaut reach), can suggest a relatively low ratio of suspended fine particulate matter to deposited fine particulate matter. It is encouraging that there were so few tolerant fauna in the riffles below the dam.

Habitat condition had mean scores that fell in the Optimal range for eight of the ten parameters, and the overall score (155) also fell just within the Optimal range. There was a lack of woody debris at our sites, and there was generally substantial coverage by filamentous green algae.

As shown in Chapter 2, the water in the Poopenaut is colder than in analogous reaches in the upper Merced River, but we did not find increases in benthic macroinvertebrate diversity or decreases in tolerance with increasing distance downstream from the dam, although the 5km study reach may have been of insufficient

length to have allowed appreciable warming before the discharged water left the study area.

Year to year variability in stream macroinvertebrate fauna can be substantial, 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. Our first year of sampling raised some questions regarding effects of river regulation on the benthic macroinvertebrate assemblage, and comparison of below-dam, above-reservoir, and unregulated reaches would be an important complement to the ongoing Looking Downstream efforts.

Response to Experimental Release

We sampled the below-dam reach one day before, one day after, and two months after the experimental release using the method outline above. We sampled fauna with kick nets, and we also added several metrics to our assessment, most importantly algal biomass. Most analysis was via 1x3 repeated measures ANOVAs.

The experimental release created striking changes in the macroinvertebrate assemblage that were apparent in all of our analyses. The flood changed an assemblage with relatively high dominance to an assemblage with greater evenness and greater proportional biodiversity. Most assemblage-level metrics showed strong responses to the release. The flood caused a five-fold reduction in algal biomass, but there was about a 50% recovery in the two months that followed. All macroinvertebrate orders decreased in abundance in association with the release as did most of the 28 families. By two months after the release, however, most taxa had again increased in

number, though most groups did not reach the densities seen before the release. Chironomid midges dominated the assemblage at the family level throughout all sampling periods despite dramatic flood losses, but the proportion of the fauna represented by these larval midges decreased in favor of more desirable taxa such as mayflies, stoneflies, and caddisflies.

The proportional contribution of collector-gatherers decreased, and all other groups increased, after the release. The strongest positive responses were demonstrated by predators, collector-filterers, and piercer-herbivores.

The release had major immediate effects on the ecology of the river, and many of these effects would be generally viewed as positive changes. The food web was clearly modified by the release. The proportion of collector-gatherers was reduced by the flood in the short term, and the collector-filterer:collector-gatherer ratio increased from a very low 0.0077 to 0.068 immediately after the flood. More importantly, this ratio was still higher than pre-flood levels two months later.

Most of the responses to the flood did lessen in the months immediately following the release, and after two months many metrics had levels between those observed immediately before and immediately after the flood. It is nonetheless 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.

As algae recolonize substrata, faunal metrics related to algal growth 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.

It is probable that both initial effects of the release and the duration of these effects would be greater in response to a release of longer duration. In general, river health will benefit from river regulation that mimics the natural pattern of flooding as closely as possible. Yosemite National Park and SFPUC are working together to plan a second of longer duration and with more gradual rising and falling hydrographic limbs. Such a release would provide a much better understanding of invertebrate-flow-habitat relationships.

There are several additional lines of investigation that would help inform management of the Tuolumne River. As noted above, comparison of below-dam, above-reservoir, and unregulated reaches should be a component of the ecological assessment of the river. Drift of benthic macroinvertebrates, in which fauna leave the substrate either actively or passively and enter the water column, is important in structuring stream assemblages and is in turn influenced by dam operations. We recommend investigation of drift in the Tuolumne system. Lastly, the seasonal wetlands perched above the river were historically inundated seasonally and almost certainly contributed significant macroinvertebrate biodiversity to the river corridor. Examining these wetland macroinvertebrate assemblages would be an important addition to the Looking Downstream initiative.

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 a spring flood event.

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), and ecological effects can cascade throughout the food web and up and down the river corridor (e.g., Holmquist et al. 1998, Greathouse et al. 2006a, b). 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).

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.

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 year of study assessed the effects of an experimental spring pulse flow on the benthic macroinvertebrate assemblage.

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, we used the US Environmental Protection Agency rapid bioassessment protocols (Barbour et al. 1999). These protocols emphasize kick netting in riffle 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 0.5m² subsamples. Although not part of the EPA protocols, we also collected some limited rock scraping samples on large rock 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/m², 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 1988), 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 $\sum(n_i a_i / N)$, where n_i = number of individuals in the i^{th} taxon, a_i = tolerance value (1-10) assigned to that taxon, and N = total number of individuals in sample with known tolerance values. 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; Sorensen 1948, 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 fines. 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, Wilkinson et al. 1992), 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; Cochran 1941, 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 (Wilkinson et al. 1992).

Response to Experimental Release

We sampled the below-dam reach one day before, one day after, and two months after the experimental release 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 flood. We sampled sites 2-5 and 7-8 (Figs. 1, 2-6, 8-9) at each of these three intervals.

We collected 1m² 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 Year 2, 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° 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 (1413 μ S/cm at 25° C), Orion perpHect buffer 7, (ph 7.00 +/-0.01 at 25° 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 1x3 repeated measures ANOVAs. 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. We examined multiple comparisons with one-tailed paired t-tests. Although all tests were *a priori* orthogonal contrasts, we desired relatively tight control of type-I error rate. We used the sequential Bonferroni adjustment (Holm 1979, Shaffer 1995, Jaccard and Guilamo-Ramos 2002), which has greater power than the standard Bonferroni adjustment (Rice 1989), to correct probability values to familywise error rates. Corrections were done in MacBonferroni (Watkins 2002).

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

was an average of 41.7 species per 2m², 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/m²= 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/m²; Table 5). *Baetis* and *Paraleptophlebia* were found in every sample.

Plecoptera were lower in abundance (individuals/m²= 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/m², respectively. Only Chloroperlidae was represented in every sample. The most abundant species were *Hesperoperla pacifica* and *Malenka* sp. (6.38 and 6.31 individuals/m², 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, respectively). Hydropsychidae and Hydroptilidae had 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/m², respectively; Table 5).

Coleoptera were relatively uncommon (4.38 individuals/m²), and Elmidae (riffle beetles) and Hydrophilidae (water scavenger beetles) were the only families collected (4.31 and 0.0625 individuals/m², 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/m², 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/m²), and in turn Chironomidae (midges; 92.1 individuals/m²) and Simuliidae (black flies; 36.2 individuals/m²) 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 8-10 (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 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/m²; Table 7). Much of this increase was driven by an increase in simuliid black flies from zero to a mean of 71.8 individuals/m² (Table 7, Fig. 12). Chironomid midges, particularly Tanytarsini, also increased from a spring-summer mean of 63.0 to a fall-winter mean of 121 individuals/m² (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/m², 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/m², 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/m², SE= 294). Adult and larval elmids (riffle) beetles were common in the same abundant sample and again absent in the other rock scrapings (mean= 276 individuals/m²; SE= 276). Diptera were also present in large numbers (mean= 104 individuals/m², SE= 68.2). Trichoptera and Plecoptera were less abundant (~50 individuals/m² each).

Response to Experimental Release

Habitat variables recorded across all three sampling periods were generally similar to those recorded during the previous year. Water depth (37.5 cm, SE= 3.10) and water temperature (mean= 7.00 °C, SE= 0.289) were almost identical to 2007-8 values (Table 2), whereas flow (mean= 57.0, SE= 5.28), stream width (mean= 25.6, 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 conductivity, pH, and total dissolved solids were 8.9 µS/cm (SE= 0.59), 6.9 (SE= 0.021), and 4.4 ppm (SE= 0.31), respectively. Tree cover averaged only 5.1% (SE= 0.98). Mean algal dry mass was 5.12 gdm/m² (SE= 0.979). Habitat condition determined via EPA Habitat Assessment protocols during the summer 2008 experiment (158) was similar to that observed during the 2007-8 initial assemblage description (155; Table 3).

In this second phase of the study, 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.

The experimental release created striking changes in the macroinvertebrate assemblage that were apparent in all of our analyses. The flood 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 (Fig. 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).

Most assemblage-level metrics showed strong responses to the release (Table 8). Overall abundance fell ten-fold from over 1000 individuals per square meter to just over 100 individuals per square meter. There was little change in family richness, but after correcting for differing abundances (Margalef's correction), family diversity peaked after the release and then fell again by two months after the release (Table 8). In contrast, species richness, with and without Margalef's correction fell following the release and did not return to pre-release richness after two months. Family dominance fell in response to the release and was still lower than pre-release levels after two months (Table 8). Percent Ephemeroptera-Plecoptera-Trichoptera (%EPT) doubled following the release and decreased but did not fall to pre-release levels (Table 8). A trend of decreasing, followed by increasing, Hilsenhoff's Biotic Index was observed, but

these effects were non-significant by a small margin. The flood caused a five-fold reduction in algal biomass, but there was about a 50% recovery in the two months that followed.

All orders decreased in abundance in association with the release (Table 9). Diptera showed the greatest flood-induced losses, falling from a mean of 892 to 61 individuals per square meter—a 93% loss. Less tolerant taxa lost density as well, but these losses were proportionally lower: 72%, 82%, and 20% for Ephemeroptera, Plecoptera, and Trichoptera (Table 9). Less abundant taxa, such as Coleoptera, Acari, and Bivalvia all had reduced densities as well. Prior to the release, Diptera dominated the assemblage at 82%; after the flood, Diptera was still the most abundant order, but this group represented only 54% of the total density.

By two months after the release, however, most taxa had again increased in number, though most groups did not reach the densities seen before the release (Table 9). Diptera rebounded to 310 individuals per square meter, or 35% of previous densities. Ephemeroptera, Plecoptera, and Trichoptera had divergent recoveries. Ephemeroptera recovered to 75% of pre-flood densities, whereas Plecoptera increased to only 19% of pre-flood densities (Table 9). In contrast, Trichoptera increased to 182% of pre-flood densities. Coleoptera had a similar response to Ephemeroptera, whereas Acari and Bivalvia densities fell still further in the two months following the release, although both of these groups were relatively uncommon before the release (Table 9). Following this two month recovery period, dipteran dominance was 75%, i.e., close to pre-flood levels. These shifts in order-level dominance parallel overall family dominance (Table 8).

Chironomid midges dominated the 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 flood and nemourids less so. Leptophlebiid mayflies ranked third, fourth, and third among families at the three different 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 flood. Ephemerellids were almost absent two months after the 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 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 release, there were some striking increases and decreases. As noted 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 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 6) for families that reached highs two months after the flood was 5.5 (SE= 0.50) but was 1.9 (SE= 0.55) for families that had reduced populations at this time.

Functional feeding groups were also affected by the experimental release. The proportional contribution of collector-gatherers decreased, and all other groups increased, after the release (Table 11). The strongest positive responses were demonstrated by predators, collector-filterers, and piercer-herbivores, increasing by a factor of four, six, and ten, respectively, although the before-after contrast was not significant for piercer herbivores due to high variance. By two months after the 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 flood (Table 11).

Discussion

Assemblage Structure

We collected a diverse assemblage of macroinvertebrates that was generally similar in character to the assemblage in the riffle habitats in the upper Merced 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 had four caddisfly families that were absent from the Tuolumne, and the Tuolumne had three caddisfly families that were absent from the Merced. The upper Merced comparison sites had four families of mites that we did not find in the upper Tuolumne, but the upper Tuolumne had one mite family that was absent from the Merced as well as 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 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. 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 1988, 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 obtained 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 instance the mean of 276 elmids/m² 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 Hetch Hetchy 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°C (mean from our 2007 September and October samples) versus 13.3°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. Deep-release dams typically reduce daily and annual temperature fluctuations and lower mean annual temperatures (Ward and Stanford 1979). These changes often lead to negative impacts on BMI diversity because of disruption of thermal cues for reproduction and development, reduction of degree days for completion of life cycles, and slowing of metabolic rates (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 Hetch Hetchy. Although diversity is often reduced in response to increased temperatures, overall production can be increased (Wohl et al. 2007). 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 5km 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). Such comparisons would be an important complement to the ongoing Looking Downstream efforts.

Response to Experimental Release

The release had major immediate effects on the ecology of the river, and many of these effects would be generally viewed as positive changes. Total abundance and all order abundances fell, 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 (Wallace 1990, Imbert and Perry 2000, Jakob 2003) and

perhaps also due to association with filamentous green algae. 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 flood—but at a lower rate than was found for other groups. There were significant but mixed effects on richness measures in our Tuolumne system. 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).

Green algal biomass was greatly reduced, 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 area being longer in length than that used by Jakob et al. (2003).

The food web was clearly modified by the release. The proportion of collector-gatherers was reduced by the flood in the short term, and the collector-filterer:collector-gatherer ratio increased from a very low 0.0077 to 0.068 immediately after the flood. More importantly, this ratio was still higher than pre-flood 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 flood. Silt deposition favors many collector-gatherers, for instance Tanytarsini (Chironomidae; Armitage 1977). 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). Prior to the 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 (0.37).

Most of the responses to the flood lessened in the months immediately following the release, as has been found in analogous studies (Jakob et al. 2003, Robinson 2003). After two months many metrics had levels between those observed immediately before and immediately after the flood. Chironomids recovered much of their abundance in the two months following the flood, and we observed increases in Baetidae and Simuliidae as was also observed by Robinson et al. (2003), although we did not observe a 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 release was a highly valuable experiment that provided a first indication of how river health might respond to an intact disturbance regime.

The differences between the Before and After samples were clearly due to the experimental flood, as sampling was done the day before and the day after the release. It is possible that some of the changes that we observed two months after the flood were due to seasonal changes or interactions with seasonal changes. The benthic macroinvertebrate assemblage did show some seasonal trends in 2007-8, although there were not major seasonal effects observed between May and July (Table 7; Figs 16-20). The slight increase in black fly (simuliid) abundance during the summer could have contributed to the higher proportion of black flies apparent two months after the release (Fig. 16). Similarly, increased family dominance in late summer could have contributed to the apparent increase in dominance two months post-release (Fig. 20). Although it seems unlikely that there were major confounding effects due to seasonality, in the absence of a control system such effects cannot be completely dismissed.

Although some effects of the release may be transitory, others are likely to persist for some time. Both periphyton and sediments are mobilized rapidly by artificial floods (Jakob et al. 2003). But, as algae recolonize substrata, faunal metrics related to algal growth 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).

It is probable that both initial effects of the release and the duration of these effects would be greater in response to a release of longer duration. 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). Yosemite National Park and SFPUC are working together to plan a second controlled release for spring of 2009. The proposed goal is a release of longer duration and with more gradual rising and falling hydrographic limbs. Such a release would provide a much better understanding of invertebrate-flow-habitat relationships, and we would sample such a release using the sampling design that we implemented for the 2008 release. 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.

There are several additional lines of investigation that would help inform management of the Tuolumne River. As outlined in the previous Discussion section, an observational study that includes not only the below-dam reach, but also above-reservoir and unregulated reaches would be a key element in developing context for current river condition. It would also be very useful to compare the assemblage below Lake Eleanor, with annual spring discharge (B. McGurk pers. comm.), with the assemblage below the Hetch Hetchy reservoir. Drift of benthic macroinvertebrates is

important in structuring stream assemblages (Wallace 1990). Both reductions and increases in flow can enhance drift, and altered drift patterns can therefore occur below dams and in other regulated systems (Irvine and Henriques 1984, 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—often entrapped by the reservoir. In turn, drift from the reach immediately below a dam may not be carried very far downstream because of reduced flows. We recommend investigation of drift in the Tuolumne system. Lastly, the 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 2005, 2006, 2008, Pierotti et al. 2008). Examining these wetland macroinvertebrate assemblages would be an important addition to the Looking Downstream initiative.

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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

Table 2. Means and standard errors for physical parameters.

<u>Metric</u>	<u>Mean</u>	<u>SE</u>
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	58.0	11.9
Percent gravel	21.0	6.40
Percent sand	13.0	3.74
Percent fines	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 (Left)	8.43	0.429	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.
(Right)	8.71	0.421	
10. Riparian Vegetative Zone Width (Left)	9.00	0.309	Optimal Width of riparian zone >18 meters; human activities (i.e., parking lots, roadbeds, clear-cuts, lawns, or crops) have not impacted zone.
(Right)	9.14	0.340	
Overall	155	5.13	Optimal

Table 4. Means and standard errors for diversity metrics.

	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

Table 5. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1° and 2° FFG), and California Tolerance Values (CTV). 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			
<i>Ameletus</i> sp.	3.00	1.20	0.750	sc	cg	0
Baetidae	60.3	21.4	1.00			
<i>Baetis</i> 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			
<i>Cinygmula</i> sp.	0.625	0.246	0.625	sc	cg	4
<i>Epeorus longimanus</i>	0.625	0.498	0.250	sc	cg	4
<i>Ironodes</i> sp.	1.44	0.759	0.500	sc	cg	4
<i>Rithrogena</i> sp.	0.875	0.875	0.125	sc	cg	0

Table 5, cont. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1^o, 2^o FFG), and California Tolerance Values (CTV). Continued next page.

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

Table 5, cont. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1^o, 2^o FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		Frequency	1 ^o FFG	2 ^o FFG	CTV
	Mean	SE				
Plecoptera, cont.						
Perlidae	8.38	3.74	0.875			
<i>Claassenia sabulosa</i>	1.81	0.647	0.625	p		3
<i>Hesperoperla pacifica</i>	6.38	3.74	0.625	p		2
<i>Hesperoperla</i> 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			
<i>Cultus tostonus</i>	0.0625	0.0625	0.125	p		2
<i>Cultus</i> sp.	0.313	0.313	0.125	p		2
<i>Osobenus yakimae</i>	0.938	0.938	0.125	p		2
<i>Skwalla americana</i>	0.125	0.125	0.125	p		2
<i>Isoperla</i> sp. A	0.250	0.250	0.125	p		2
<i>Isoperla</i> sp. B	0.188	0.188	0.125	p		2
Chloroperlidae	7.31	3.05	1.00			
<i>Alloperla</i> sp.	0.250	0.250	0.125	p		1
<i>Haploperla chilnualna</i>	1.13	0.603	0.625	p	cg	1
<i>Plumiperla</i> sp.	0.938	0.868	0.250	p		1
<i>Suwallia</i> sp. A	3.00	1.46	0.625	p		1
<i>Suwallia</i> sp. B	1.94	1.45	0.250	p		1
Unknown	0.0625	0.0625	0.125	p		1

Table 5, cont. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1^o, 2^o FFG), and California Tolerance Values (CTV). Continued next page.

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

Table 5, cont. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1^o, 2^o FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		Frequency	1 ^o FFG	2 ^o FFG	CTV
	Mean	SE				
Coleoptera	4.38	2.27	0.625			
Hydrophilidae	0.0625	0.0625	0.125			
<i>Enochrus</i> sp. (a)	0.0625	0.0625	0.125	ph		5
Elmidae	4.31	2.28	0.625			
<i>Cleptelmis addenda</i> (l)	2.25	1.97	0.375	cg	sc	4
<i>Cleptelmis addenda</i> (a)	0.0625	0.0625	0.125	cg	sc	4
<i>Heterlimnius</i> sp. (l)	0.250	0.250	0.125	cg	sc	4
<i>Optioservus quadrimaculatus</i> (a)	1.25	0.366	0.625	cg		4
<i>Rhizelmis nigra</i> (l)	0.375	0.375	0.125	sc	cg	2
<i>Zaitzevia</i> 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			
<i>Pericoma</i> sp.	0.0625	0.0625	0.125	cg		4
Simuliidae	36.2	14.6	0.750			
<i>Simulium</i> spp.	36.1	14.5	0.750	cf		6
<i>Simulium canadense</i> (pu)	0.0625	0.0625	0.125	cf		6

Table 5, cont. Densities (per m²; SE= standard error) and frequency of occurrence of taxa, primary and secondary functional feeding groups (1^o, 2^o FFG), and California Tolerance Values (CTV). Continued next page.

	Abundance		Frequency	1 ^o FFG	2 ^o FFG	CTV
	Mean	SE				
Diptera, cont.						
Tipulidae	2.25	0.835	0.750			
<i>Antocha</i> sp.	0.125	0.0818	0.250	cg		3
<i>Dicranota</i> sp.	1.25	0.866	0.250	p		3
<i>Hexatoma</i> sp.	0.875	0.515	0.375	p		2
Empididae	1.06	0.427	0.500			
<i>Clinocera</i> sp.	0.188	0.188	0.125	p		6
<i>Hemerodromia</i> sp.	0.438	0.371	0.250	p		6
<i>Wiedemannia</i> sp.	0.0625	0.0625	0.125	p		6
<i>Clinocera/Wiedemannia</i> (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			
<i>Hydrachna</i> 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 m²; 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				
Mollusca, Bivalvia						
Veneroida	0.875	0.806	0.250			
Sphaeriidae	0.875	0.806	0.250			
<i>Sphaerium</i> 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

Table 6. Mean percentage of fauna (by individuals) and standard errors for primary functional feeding groups.

	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

Table 7. Mean values (SE= standard error) for selected metrics as a function of period during which sampling occurred: Spring-Summer (March through August) or Fall-Winter (September through February). 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		p
	Mean	SE	Mean	SE	
Diptera	66.9	27.9	196	18.6	0.0209
<i>Simulium</i> sp.	0.500	0.354	71.8	11.9	0.0202
<i>Serratella teresa</i>	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

Table 8. Response of mean (SE) macroinvertebrate assemblage-level variables and algal biomass to experimental release (all per-square-meter). %EPT= percent Ephemeroptera + Plecoptera + Trichoptera. The ANOVA column contains p-values for 1x3 repeated measures ANOVAs. The three columns representing the three possible multiple comparisons contain p-values resulting from one-tailed t-tests. Asterisks represent significance at two different error rates: * represents $p < 0.05$ at the per contrast error rate; ** represents $p < 0.05$ after correction to family-wise error rate via the sequential Bonferroni inequality.

	Before		After		2 mo after		ANOVA	Before-After	After-2 mo after	Before-2 mo after
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE				
Total Individuals	1086	287	112	34	415	123	0.0037	0.0036**	0.038**	0.024**
Family Richness	16.3	0.494	13.2	1.68	12.7	1.33	0.063	0.064	0.33	0.031*
Margalef's Corrected Family Richness	2.25	0.0584	2.74	0.169	2.051	0.269	0.015	0.0036**	0.0090**	0.15
Species Richness	42.8	2.48	22.7	3.22	29.0	3.11	0.0036	0.0042**	0.069	0.016**
Margalef's Corrected Species Richness	6.13	0.258	4.83	0.316	4.86	0.483	0.033	0.0033**	0.44	0.030*
% Family Dominance	77.6	3.61	47.8	5.51	61.1	8.00	0.018	0.0025**	0.14	0.045*
% EPT	20.5	3.35	44.3	5.52	32.7	6.72	0.018	0.0013**	0.11	0.075
Hilsenhoff's Biotic index	5.47	0.0876	4.97	0.287	5.49	0.149	0.098	0.055	0.077	0.48
Algal Biomass (gdm)	9.00	1.99	1.91	0.590	4.46	0.561	0.00029	0.0011**	0.00085**	0.035**

Table 9. Response of mean (SE) macroinvertebrate order densities per meter square to experimental release. The ANOVA column contains p-values for 1x3 repeated measures ANOVAs. The three columns representing the three possible multiple comparisons contain p-values resulting from one-tailed t-tests. Asterisks represent significance at two different error rates: * represents $p < 0.05$ at the per contrast error rate; ** represents $p < 0.05$ after correction to family-wise error rate via the sequential Bonferroni inequality.

	Before		After		2 mo after		ANOVA	Before-After	After-2 mo after	Before-2 mo after
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE				
Ephemeroptera	90.8	14.6	25.2	7.76	67.7	17.1	0.0063	0.0087**	0.021**	0.11
Plecoptera	86.2	25.9	15.7	5.48	16.8	4.62	0.012	0.017*	0.18	0.028*
Trichoptera	10.0	2.31	8.00	2.35	18.2	5.96	0.13	0.22	0.066	0.058
Coleoptera	2.83	1.014	0.833	0.401	2.17	0.703	0.11	0.023*	0.045*	0.37
Diptera	892	260	61.0	21.2	310	112	0.0028	0.0022**	0.038**	0.025**
Acari	2.17	1.078	0.833	0.477	0.167	0.167	0.19	0.20	0.15	0.053
Veneroidea (Bivalvia)	2.00	1.18	0.833	0.833	0.667	0.422	0.34	0.079	0.39	0.19

Table 10. Response of mean (SE) macroinvertebrate densities per meter square to 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
<i>Ameletus</i> sp.	5.33	2.96	0.667	0.667	0	0
Baetidae	16.8	5.77	11.5	3.73	48.2	13.9
<i>Baetis</i> 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
<i>Cinygmula</i> sp.	2.67	1.02	0.167	0.167	1.17	0.601
<i>Epeorus longimanus</i>	3.67	1.98	0.500	0.342	0	0
<i>Epeorus</i> sp.	0.500	0.500	0.167	0.167	0	0
<i>Ironodes</i> 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
<i>Caudatella hystrix</i>	1.83	1.05	0.833	0.543	0	0
<i>Ephemerella excrucians</i>	5.33	1.61	1.33	1.151	0	0
<i>Ephemerella dorothea infrequens</i>	7.50	4.75	2.33	1.94	0	0
<i>Ephemerella</i> sp. A	0.500	0.500	0.500	0.500	0	0
<i>Serratella teresa</i>	6.50	0.719	0	0	0	0
<i>Serratella micheneri</i>	0	0	0	0	0.167	0.167

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 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
<i>Paraleptophlebia</i> sp. A	35.5	6.78	5.67	3.03	4.00	2.71
<i>Paraleptophlebia</i> 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
<i>Malenka</i> 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
<i>Claassenia sabulosa</i>	0.333	0.211	0.667	0.667	0.333	0.333
<i>Hesperoperla pacifica</i>	9.17	2.94	1.33	0.715	0.833	0.654
<i>Hesperoperla</i> sp.	0	0	0.500	0.342	0.167	0.167
Perlodidae	3.00	0.775	0.667	0.211	0.333	0.333
<i>Osobenus yakimae</i>	3.00	0.775	0.667	0.211	0	0
<i>Skwalla americana</i>	0	0	0	0	0.333	0.333
Chloroperlidae	0.500	0.342	1.67	1.31	1.33	1.33
<i>Haploperla chilnualna</i>	0.167	0.167	0.167	0.167	1.33	1.33
<i>Plumiperla</i> sp.	0.167	0.167	1.17	1.17	0	0
<i>Paraperla</i> sp.	0.167	0.167	0	0	0	0
<i>Suwallia</i> sp. A	0	0	0.333	0.333	0	0

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 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
<i>Orohermes crepusculus</i>	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
<i>Dolophilodes</i> sp.	0	0	0	0	1.00	0.632
Polycentropodidae	1.17	0.980	1.33	1.15	3.50	2.50
<i>Polycentropus</i> sp.	1.17	0.980	1.33	1.15	3.50	2.50
Hydropsychidae	3.17	2.07	2.17	1.33	0	0
<i>Hydropsyche</i> sp.	3.17	2.07	2.17	1.33	0	0
Rhyacophilidae	2.17	0.703	1.00	0.516	0.833	0.307
<i>Rhyacophila</i> sp. A	1.50	0.563	0.667	0.494	0.500	0.224
<i>Rhyacophila</i> sp. B	0.167	0.167	0.333	0.211	0.167	0.167
<i>Rhyacophila</i> sp. C	0.167	0.167	0	0	0	0
<i>Rhyacophila</i> 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 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
<i>Hydroptila</i> sp. A	1.00	0.817	0	0	11.3	5.28
<i>Hydroptila</i> sp. B	1.50	0.806	1.83	0.703	0.167	0.167
<i>Hydroptila</i> 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
<i>Lepidostoma</i> sp.	0.833	0.401	1.50	1.02	1.00	0.632
Limnephilidae	0	0	0.167	0.167	0	0
<i>Psychoglypha</i> 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
<i>Haliplus</i> sp. (a)	0	0	0	0	0.167	0.167
Dytiscidae	0.167	0.167	0.167	0.167	0.333	0.211
<i>Hygrotus</i> sp. (l)	0.167	0.167	0	0	0	0
<i>Laccophilus</i> sp. (a)	0	0	0	0	0.167	0.167
<i>Neoclypeodytes</i> sp. (l)	0	0	0.167	0.167	0	0
<i>Uvarus</i> sp. (a)	0	0	0	0	0.167	0.167
Hydraenidae	0.167	0.167	0	0	0	0
<i>Hydraena</i> sp. (a)	0.167	0.167	0	0	0	0

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 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
<i>Ampumixis</i> sp. (l)	0.167	0.167	0	0	0	0
<i>Cleptelmis addenda</i> (l)	0.667	0.333	0	0	0.333	0.333
<i>Cleptelmis addenda</i> (a)	0.167	0.167	0	0	0	0
<i>Optioservus quadrimaculatus</i> (l)	0.500	0.224	0.167	0.167	0	0
<i>Optioservus quadrimaculatus</i> (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
<i>Simulium</i> 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
<i>Antocha</i> sp.	0.833	0.543	0.167	0.167	0	0
<i>Dicranota</i> sp.	0	0	0	0	0.167	0.167
<i>Hexatoma</i> sp.	0	0	0.167	0.167	0	0
<i>Limonia</i> sp.	0	0	0	0	0.167	0.167

Table 10 (cont.). Response of mean (SE) macroinvertebrate densities per meter square to 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
<i>Chelifera</i> sp.	0.333	0.211	0.167	0.167	4.17	2.02
<i>Clinocera</i> sp.(I)	5.33	3.61	2.17	0.946	0	0
<i>Clinocera</i> sp. pupa	0.167	0.167	0	0	0	0
<i>Hemerodromia</i> 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
<i>Sperchon</i> 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
<i>Sphaerium</i> 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

Table 11. Response of functional feeding groups to experimental release. The ANOVA column contains p-values for 1x3 repeated measures ANOVAs. The three columns representing the three possible multiple comparisons contain p-values resulting from one-tailed t-tests. Asterisks represent significance at two different error rates: * represents $p < 0.05$ at the per contrast error rate; ** represents $p < 0.05$ after correction to family-level error rate via the sequential Bonferroni inequality.

	Before		After		2 mo after		ANOVA	Before-After	After-2 mo after	Before-2 mo after
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE				
% Scrapers	1.90	0.640	2.54	0.946	0.546	0.182	0.061	0.26	0.039*	0.036*
% Predators	2.96	0.596	12.1	3.66	3.67	1.11	0.0061	0.011**	0.015**	0.29
% Collector-Gatherers	86.8	1.48	65.5	5.49	82.1	4.72	0.026	0.010**	0.061	0.16
% Shredders	7.57	1.09	11.1	2.73	5.86	1.89	0.057	0.081	0.023*	0.13
% Collector-Filterers	0.670	0.193	4.48	1.74	4.77	1.69	0.11	0.037*	0.47	0.017*
% Piercer-Herbivores	0.354	0.155	3.61	2.39	3.28	1.31	0.21	0.076	0.44	0.041*

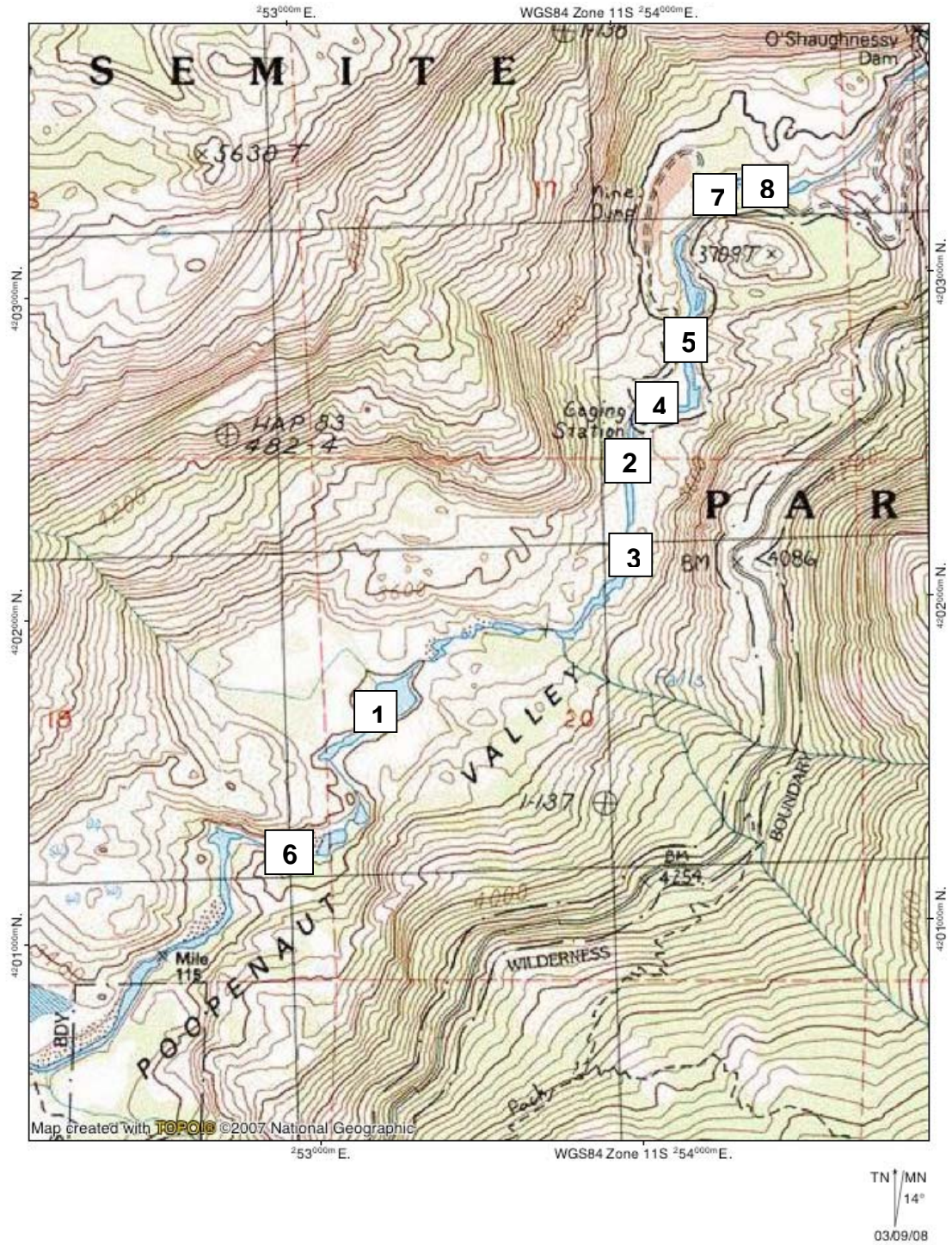


Fig.1. Location of sampling sites.



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).

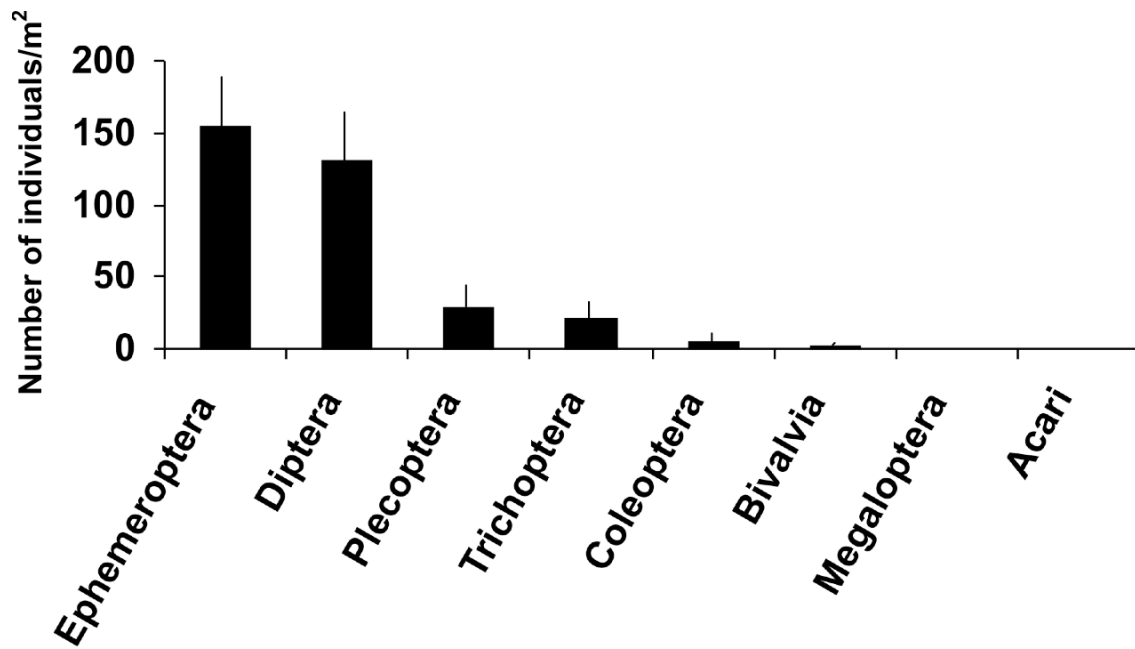


Fig. 6. Rank-abundance by order, plus Class Bivalvia (linear scale).

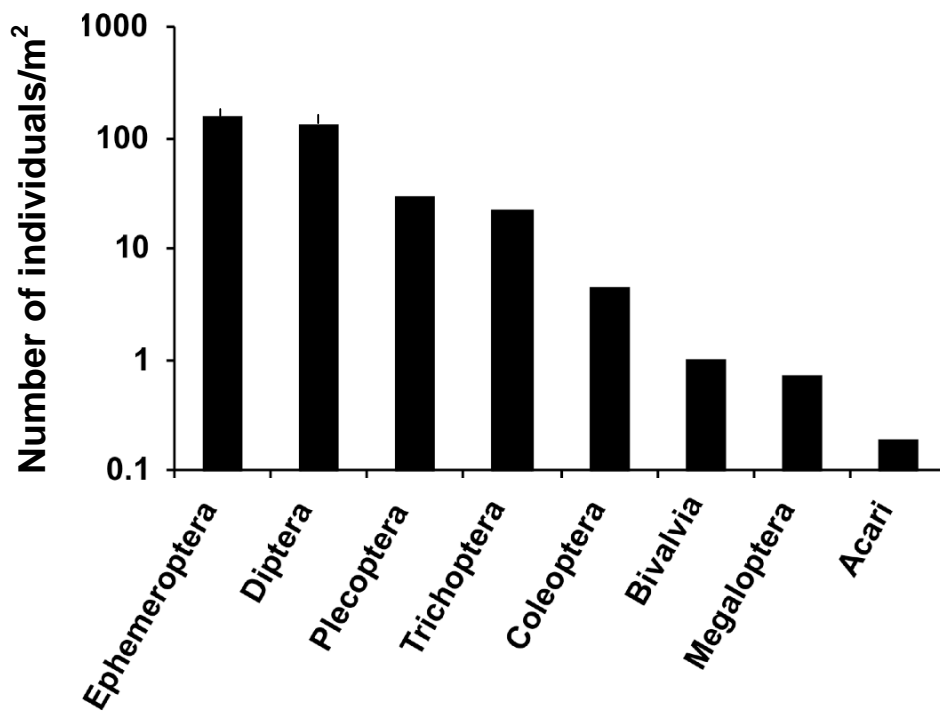


Fig. 7. Rank-abundance by order, plus Class Bivalvia (log scale).

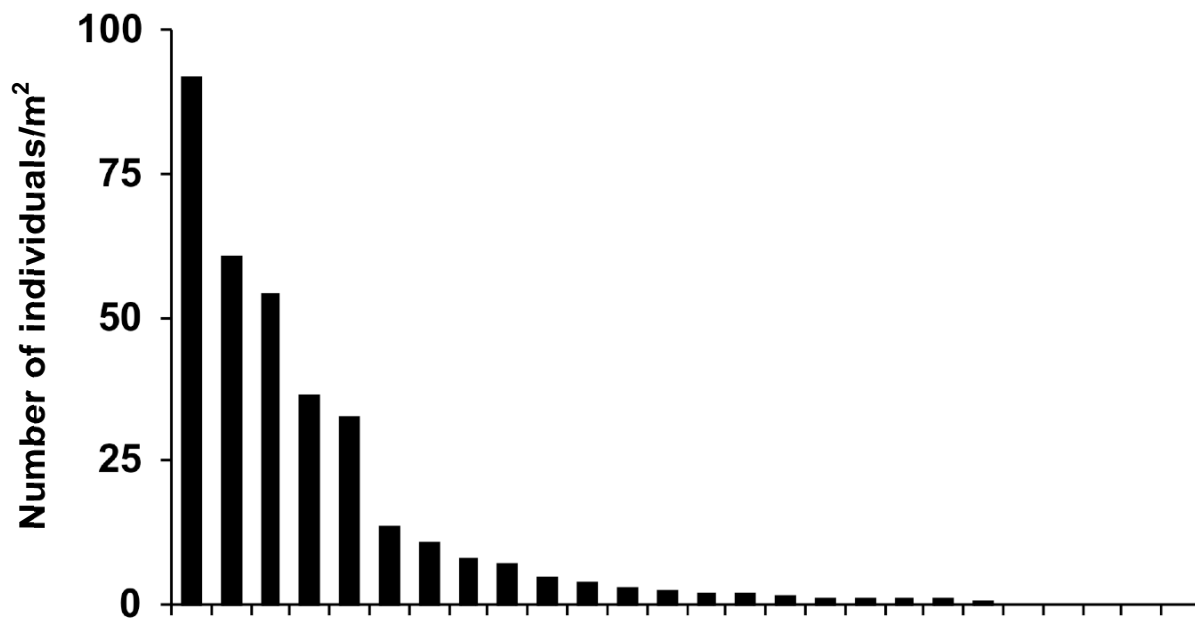


Fig 8. Rank-abundance by family (linear scale).

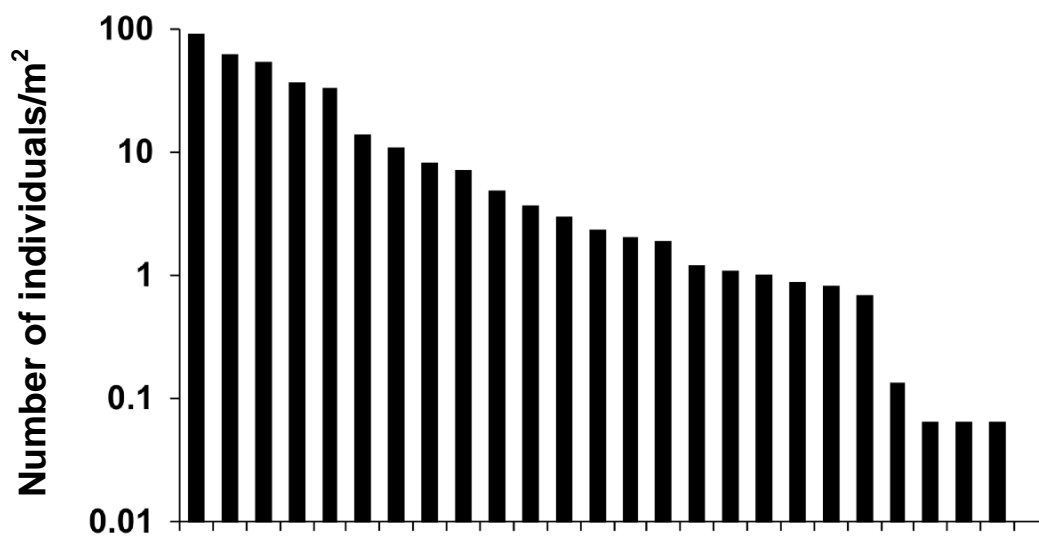


Fig. 9. Rank-abundance by family (log scale).

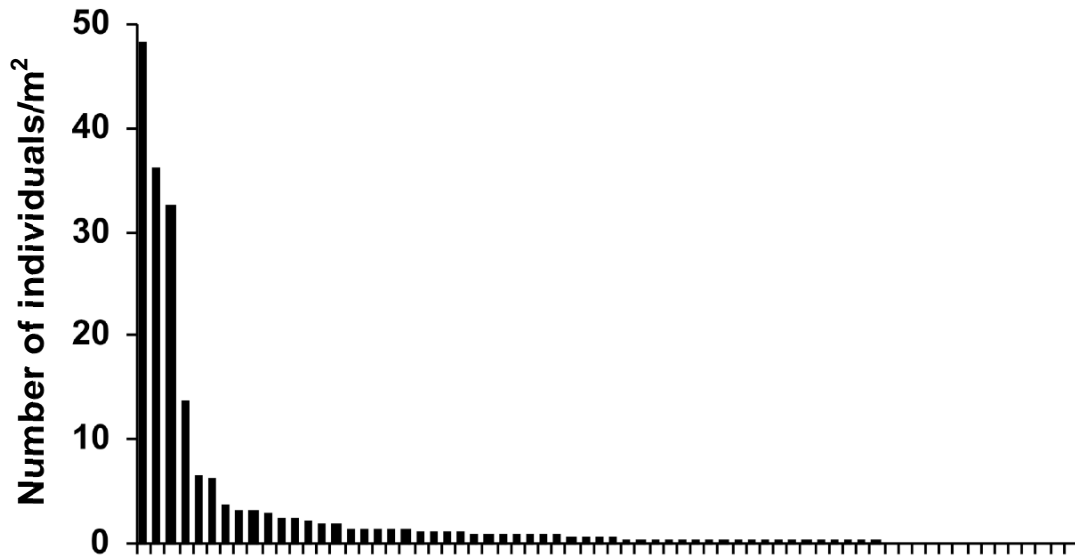


Fig 10. Rank-abundance at the species level (linear scale).

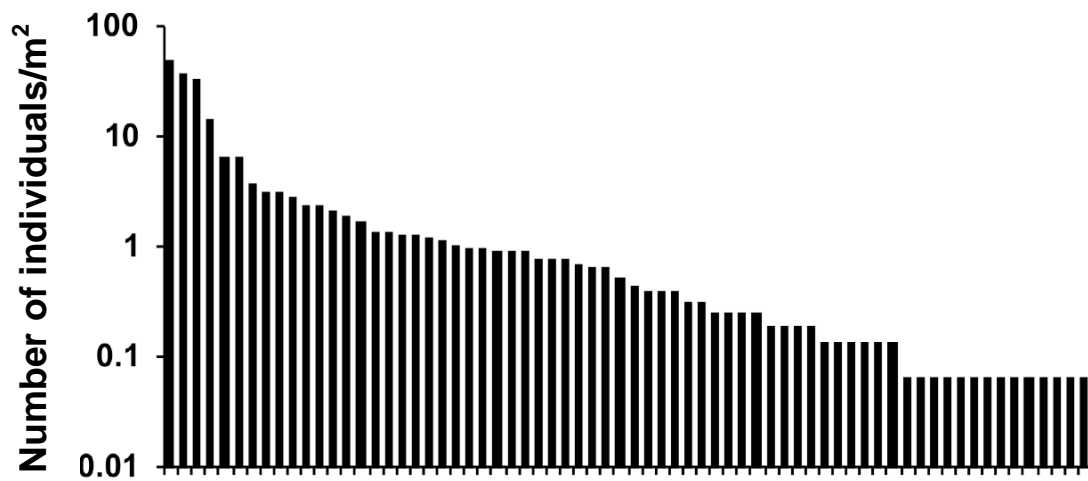


Fig 11. Rank-abundance at the species level (log scale).

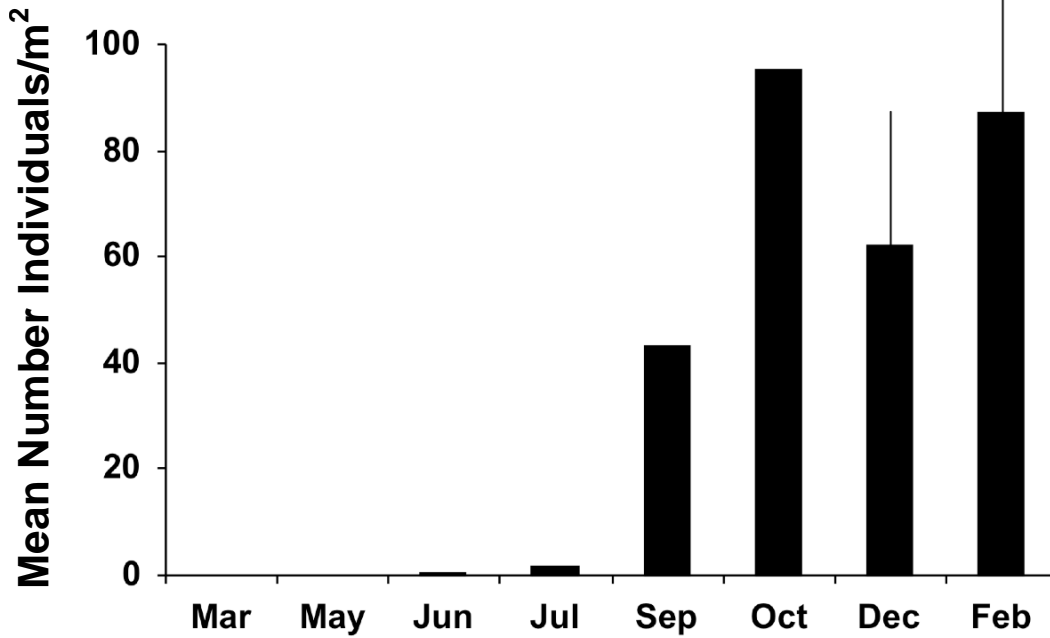


Fig. 12. *Simulium* (black flies; Diptera: Simuliidae) densities during study year.

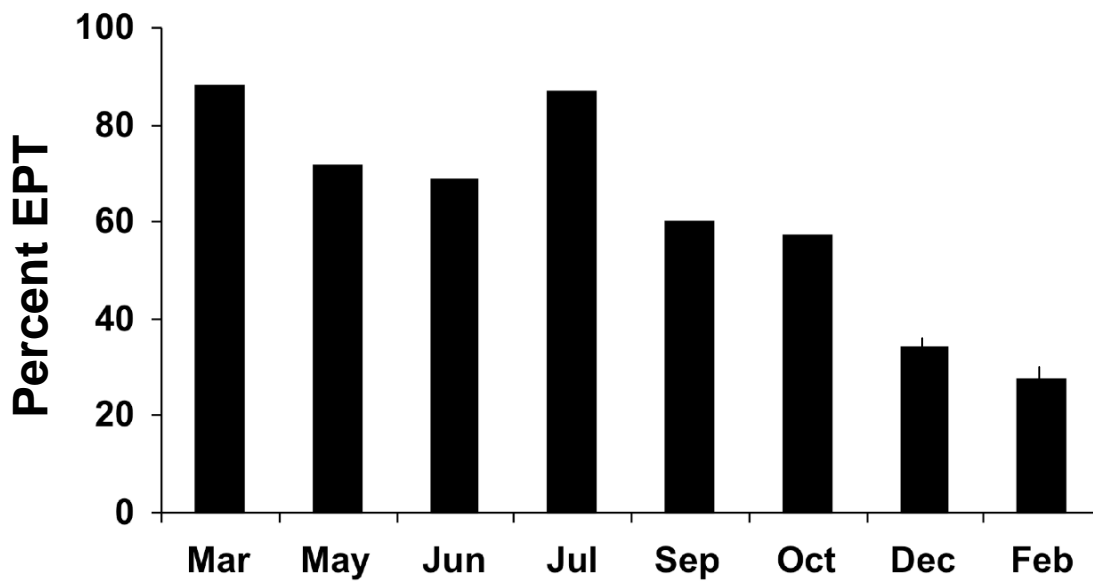


Fig. 13. Percent Ephemeroptera-Plecoptera-Trichoptera during study year.

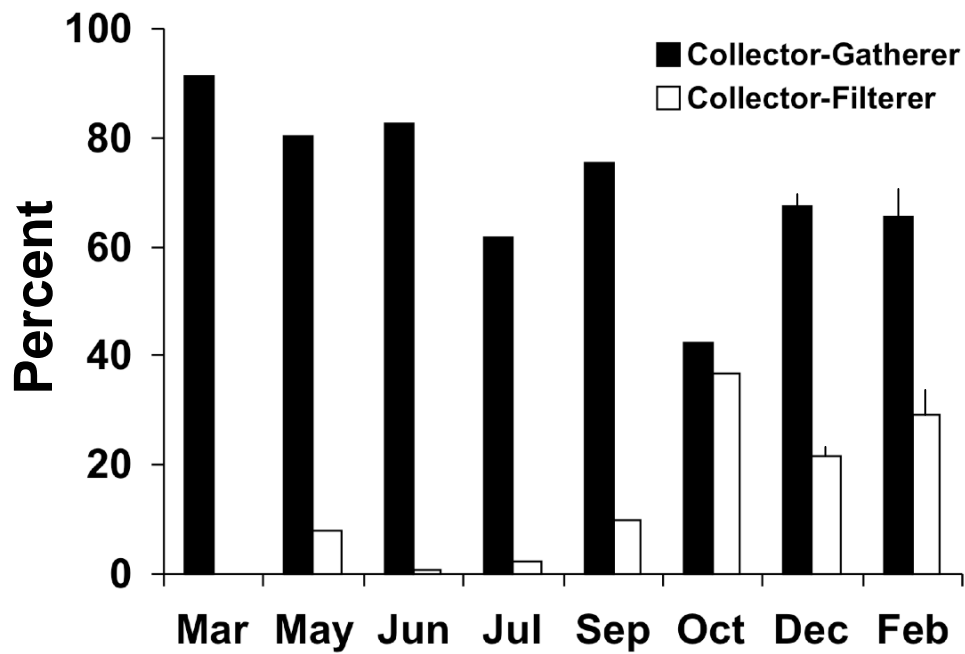


Fig. 14. Percent Collector-Gatherers and Collector-Filterers during study year.

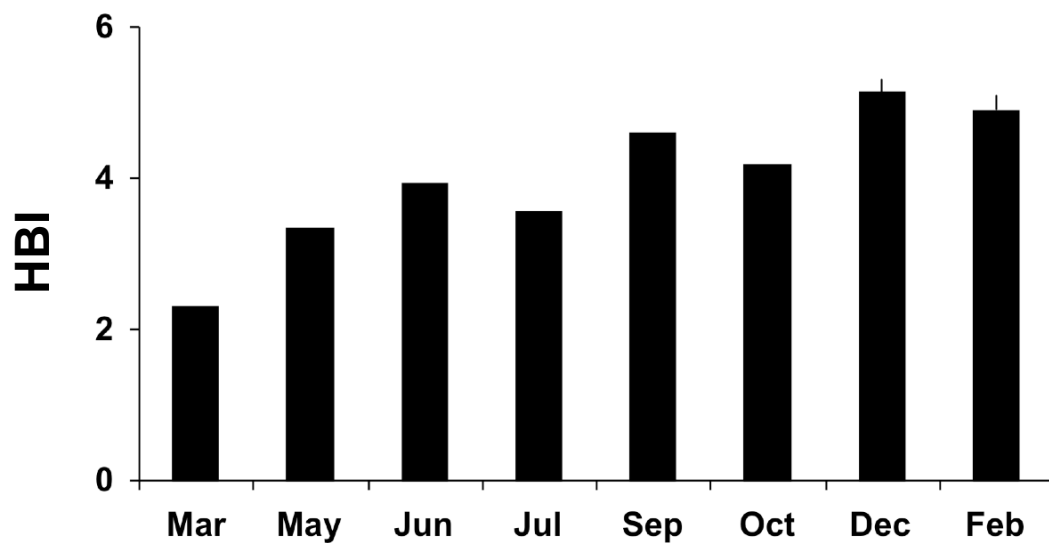


Fig. 15. Hilsenhoff Biotic Index during study year.

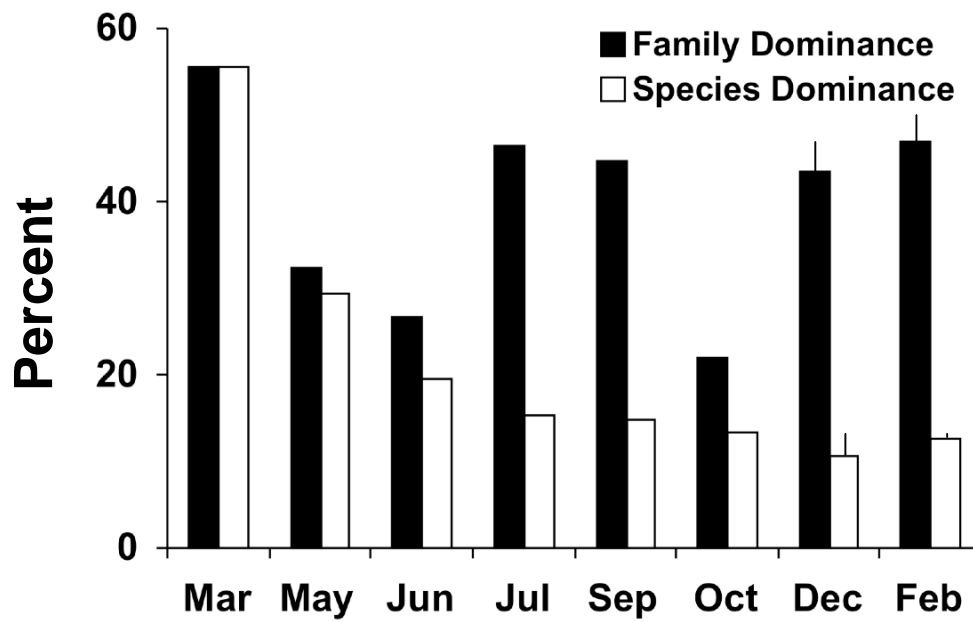


Fig. 16. Percent Family and Species Dominance during study year.

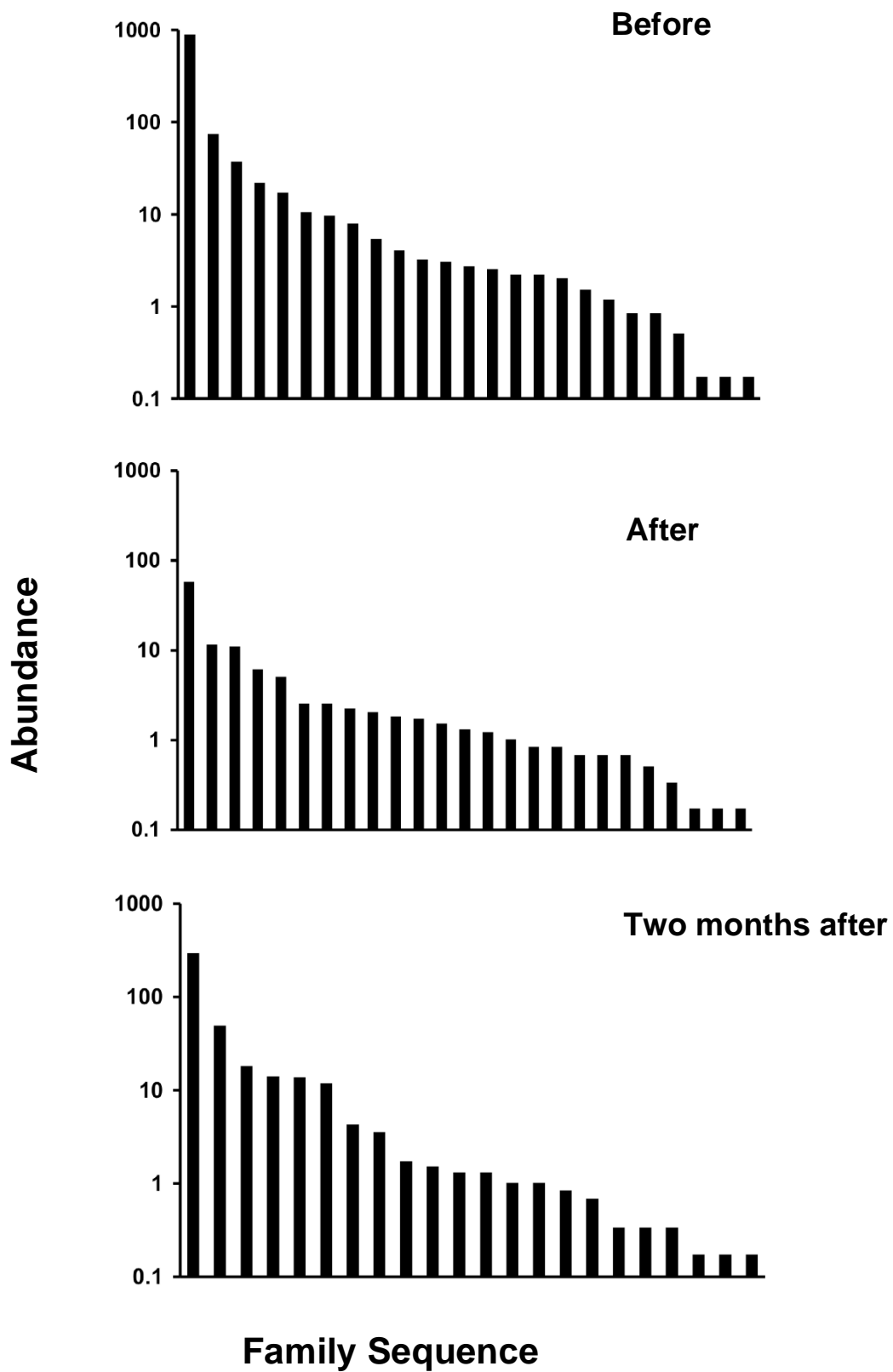


Fig. 17. Rank-abundance by sampling event at the family level (log scale).

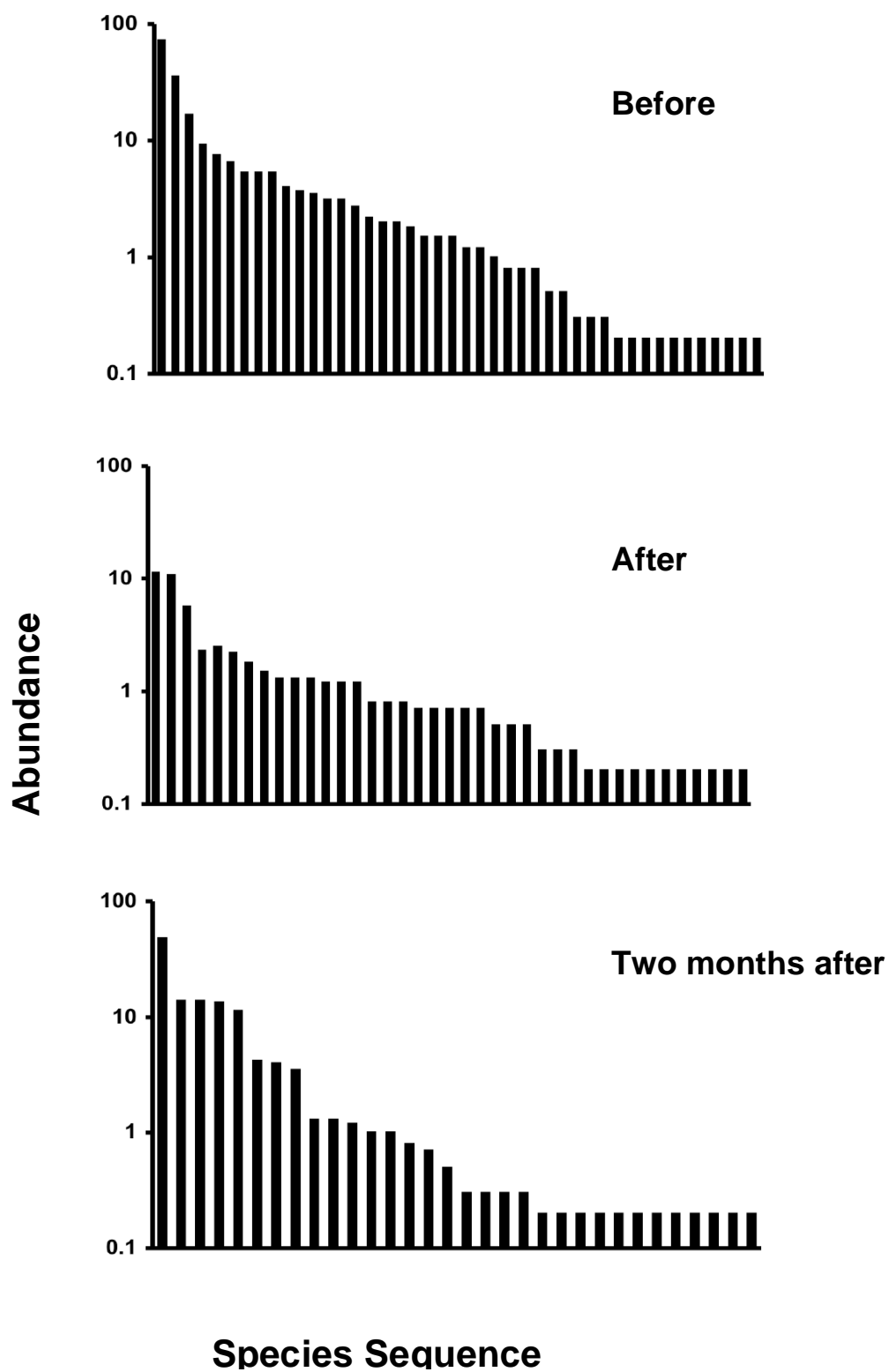


Fig. 18. Rank-abundance by sampling event at the species level (log scale).