EFFECTS OF WILDFIRE ON AQUATIC INSECT ASSEMBLAGES, EMERGING ADULT INSECTS, AND RIPARIAN CONSUMERS IN A WILDERNESS WATERSHED

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To the
DeVlieg Foundation:

Thank you for all the
support that made this
thesis possible.
Rachel J Malison

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ADULT INSECTS, AND RIPARIAN CONSUMERS IN A WILDERNESS

WATERSHED

by

Rachel L. Malison

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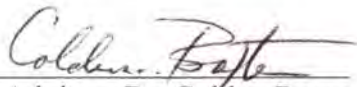
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To the Graduate Faculty:

The members of the committee appointed to examine the thesis of
RACHEL L. MALISON find it satisfactory and recommend that it be accepted.

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EFFECTS OF WILDFIRE ON AQUATIC INSECT ASSEMBLAGES, EMERGING ADULT INSECTS, AND RIPARIAN CONSUMERS IN A WILDERNESS WATERSHED

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ABSTRACT

Wildfire is an important natural disturbance and has the potential to alter linkages between land and water, yet relatively few studies have addressed its influences on stream ecosystems or the vectors of aquatic-terrestrial connectivity. I investigated the midterm effects of wildfire on periphyton, benthic and emerging adult aquatic insects, spiders and bats, and composition of benthic and emergence insect assemblages. I compared unburned sites to those that experienced low-severity versus high-severity wildfire to investigate whether fire severity might mediate the response of stream-riparian zones to wildfire. Although I observed no difference in periphyton chlorophyll a, I did observe the greatest biomass of benthic insects, greatest flux of emerging adult insects, and greatest number of spiders and bat echolocation calls at sites which experienced high severity fire. My results suggest that high severity wildfire may lead to an extended "fire-pulse" that stimulates aquatic productivity and the flux of aquatic prey to terrestrial habitats, driving local increases in riparian consumers.

DEDICATION

I would like to dedicate this thesis to Mr. Richard Hanna, my high school science teacher. Thanks to his dedication and enthusiasm I decided to pursue a career in science.

CHAPTER 1

THE "FIRE PULSE:" WILDFIRE STIMULATES FLUX OF AQUATIC PREY TO TERRESTRIAL HABITATS AND DRIVES INCREASES IN RIPARIAN CONSUMERS

INTRODUCTION

Wildfire is among the most important natural disturbances in watersheds of western North America. In the past several decades ecologists have realized that fire plays an important role in ecosystem structure and function. The effects of wildfire may grow as climate drives increases in large-wildfire frequency and longer fire seasons (Westerling et al. 2006). Many studies have investigated the role of wildfire in terrestrial systems (Agee 1993, Halpern and Spies 1995, Bailey and Whitham 2002) and the role of wildfire in aquatic systems has begun to receive more attention (Minshall et al. 1989, Greswell 1999, Bisson et al. 2003). However, the effects of wildfire on the ecological linkages between land and water have not been the focus of study.

Fire has the potential to alter land-water linkages, yet relatively few studies have addressed its influences on stream ecosystems or the vectors of aquatic-terrestrial connectivity (Bisson et al. 2003, Dwire and Kauffman 2003). Streams and rivers are closely linked to their adjacent riparian zones and upland habitats by flows of materials, energy, and organisms. Land-to-water fluxes including nutrients, leaves, and woody debris are well documented (Minshall 1967, Likens and Bormann 1974, Hynes 1975), and new work has highlighted the role of terrestrial invertebrates that fall into streams and become prey for fish (Wipfli 1997, Nakano et al. 1999, Baxter et al. 2005). Recently it has been demonstrated that reciprocal flows of energy and nutrients from water to land

can feed terrestrial organisms (Polis et al. 2004). For example, the emergence of adult insects from streams may constitute a substantial export of energy to terrestrial food webs, fueling consumers such as birds, bats, lizards, and spiders (Nakano and Murakami 2001, Power et al. 2004, Baxter et al. 2005). As a result of such connectivity, streams and their adjacent riparian zones are coupled in their responses to natural disturbances, including wildfire.

The effects of wildfire on stream-riparian ecosystems typically vary with time after a fire. Minshall et al. (2004) categorized four stages of watershed response and recovery following fire as: (1) immediate (the time of active burning to a few days after), (2) short-term (a few days to the beginning of spring run-off), (3) mid-term (usually from spring runoff of the 1st post-fire year to sometime beyond the 10th year), and (4) long-term (occurring decades or centuries later). Most of the studies done on the effects of wildfire on stream-riparian ecosystems have focused on the immediate and short-term time period responses. Understanding the role of wildfire in watersheds also requires investigation of mid- to long-term responses to this natural disturbance.

In the mid-term time frame wildfire has the potential to stimulate aquatic production. In contrast for immediate and short-term effects, in the mid-term wildfire may contribute to greater biomass and production of stream insect larvae (Minshall et al. 1989). The basis for this increase in productivity may be faster algal growth in streams with removed canopy, higher temperatures, or increased delivery of inorganic nutrients such as nitrogen and phosphorus (Spencer and Hauer 1991, Robinson et al. 1994, Minshall et al. 1997). An increase in stream primary production may drive increases in secondary production of herbivorous stream insect larvae (Minshall 2003). On the other

hand, effects of fire might diminish benthos via habitat disturbance (e.g. debris flows, increased sedimentation). If benthic larvae were stimulated, this should translate to more adult insects emerging from burned streams compared to unburned streams. However, this hypothesized bottom-up pulse in aquatic productivity driven by wildfire has not been investigated.

Consumers specializing on riparian insects may also benefit from a pulse in productivity following wildfire. Emerging stream insects can contribute anywhere from 25-100% of the energy or carbon required by riparian consumers (Baxter et al. 2005). For example, some guilds of web-weaving and ground-dwelling spiders derive the majority of their carbon from emerging stream insects (Power and Rainey 2000, Collier et al. 2002, Paetzold et al. 2005). In particular, spiders of the family Tetragnathidae build horizontal webs in riparian zones and are dependent on emerging insects for a large portion of their diet (Williams et al. 1995, Kato et al. 2004), and their abundance tracks spatial variation in insect emergence (Kato et al. 2003, Baxter et al. 2004, Iwata 2006). Similarly, bats that forage on emerging aquatic insects have also been shown to track changes in availability of this resource (Power et al. 2004, Fukui et al. 2006).

Fire severity may mediate the strength of the pulse of aquatic prey to terrestrial habitats. In terrestrial systems, more severe fires have stronger effects on forest and grassland structure and composition (Agee 1993, Halpern and Spies 1995, Turner et al. 1997, Dwire and Kauffman 2003). Furthermore, the response to fire severity is often incremental, with high severity fires having the greatest effects, unburned areas experiencing no effects, and low severity fires falling intermediate, but more similar to areas which experienced high severity fire (see Halpern and Spies 1995). In some cases,

severe fires are more likely to increase both primary and secondary productivity and affect higher trophic levels, compared to mild fires (see Singer and Harter 1996, Bailey and Whitham 2002). Just as more severe fires have different effects on terrestrial ecosystems than mild fires, different responses may be noted at the aquatic-terrestrial interface. However, few studies have investigated the effects of fire severity on linked stream-riparian ecosystems.

In this study, I sought to examine the effects of wildfire in the mid-term, 5-10 years post-fire, on the productivity of streams and consequences for riparian predators of stream insects. I hypothesized that wildfire would result in an extended fire-pulse by stimulating aquatic productivity and the flux of aquatic prey to terrestrial habitats, driving an increase in riparian consumers in the mid-term period. To test this hypothesis, I compared various food web components in a suite of unburned watersheds to those that had experienced low-severity and high-severity wildfire. I measured responses across 3 trophic levels: biomass of periphyton (attached stream algae), benthic invertebrates, emerging adult aquatic insects, and occurrence of spiders and bats. I tested four predictions: (a) periphyton chlorophyll a would be greater in burned vs. unburned sites, (b) biomass of benthic invertebrates would be greater in burned vs. unburned sites, (c) the flux of emerging adult aquatic insects would be greater in burned vs. unburned sites, and (d) the frequency of occurrence of spiders and bats would be greater at burned vs. unburned sites. In addition, I hypothesized that the effects of wildfire would be incremental, such that sites that experienced high severity fire would have the highest periphyton biomass, secondary productivity and occurrence of riparian consumers, whereas low severity sites would fall intermediate relative to unburned sites. Thus, this

field study was unique that I examined the effects of fire and fire severity on both aquatic and terrestrial organisms.

METHODS

Study Site

Study streams were located within the Payette National Forest in central Idaho, on tributaries of Big Creek, which flows into the Middle Fork of the Salmon River in the Frank Church 'River of No Return' Wilderness Area. I chose to study the effects of wildfire in this wilderness watershed because I wanted to measure responses by stream ecosystems mostly unaltered by humans, and also because here natural fire regimes have been minimally affected by fire suppression or land cover change. The Big Creek drainage experienced the intense 'Diamond Wildfire' in 2000 which burned most of the lower portion of the drainage. This region has also been affected to varying degrees by other fires including the Golden Fire of 1988, the Rush Point Fire of 1991, and the Dunce Fire of 2006. The streams flow through steep, narrow valleys with forested slopes, a mixture of primarily Douglas-Fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*). Additionally, bare and sparsely vegetated areas of grass and sagebrush (*Artemisia*) are common. The dominant riparian vegetation includes Red Osier Dogwood (*Cornus sericea*), Rocky Mountain Maple (*Acer glabrum*) and Alder (*Alnus viridis*). The region receives an average of 40 cm of precipitation annually, the majority falling as snow, resulting in peak flows from late spring through mid-summer. The streams generally remain at baseflow conditions from late summer through winter.

I limited my choice of study streams to those affected by the 2000 Diamond fire, with similar unburned streams serving as controls. Based on the condition of the riparian vegetation in 2005, I categorized reaches in the lower Big Creek drainage into three classes (Fig. 1.1): (1) 'high severity burn,' where wildfire removed both riparian understory and canopy, and presently only the understory has returned; (2) 'low severity burn,' where fire removed the understory but not canopy, and the understory has returned under an intact canopy; and (3) 'unburned,' where the reach was entirely unburned or burned long ago (>50 years). Due to the large spatial extent and high severity of the Diamond fire, my study design was unbalanced, with six high severity reaches, three low severity reaches, and three unburned reaches. This design was necessary as it was impossible to find additional unburned and low severity burned study reaches suitably close by for repeated sampling on foot. Ten of the 12 study streams were located in separate sub-drainages (Fig. 1.2). All study reaches were 100 m in length, and selected based on segment and reach classification (*sensu* Frissell et al. 1986, Bisson et al. 2006) to ensure similar stream size (2nd-3rd order), valley segment type (alleviated canyon), and reach type (step-pool, Bisson et al. 2006). Selected reaches were stratified by channel units (pools, riffles) and samples taken systematically from within these strata. For the field season of 2006 four additional reaches, two unburned (2nd and 3rd order) and two high severity burned (3rd and 5th) (Fig. 1.2), were included in the study to make additional measurements of periphyton and spider abundance.

Sampling

I sampled the 12 reaches from May through October 2005, with additional samples collected on 16 reaches in June and July 2006. At each site, I collected data on a

suite of physical and biological parameters following the methods of long-term monitoring studies conducted in this area by Minshall and his colleagues (see Davis et al. 2001).

I collected data on a range of physical factors that I anticipated might affect production within the linked aquatic-terrestrial foodweb. These habitat variables included solar radiation, aspect, temperature, stream width and depth, streambed substrate conditions, and available structure for spider web attachment. Influx of solar energy can be an important factor in determining the productivity of a stream. I estimated solar input at each site between 12:00 and 14:00 on cloudless days during July 2006. Potential solar input was measured at four locations along each reach, every 25m, using a Solar Pathfinder which measures the available annual solar radiation as constrained by topographic features (Solar Pathfinder [Solar Pathfinder, Linden, TN, USA, www.solarpathfinder.com]). In addition, I took 20 measures of PAR (Light meter [LI-COR, Lincoln, NE, USA]) (every 2 meters) starting at the beginning of each reach, just above the water surface. I took the measurement within the dominant type of light present (i.e. direct sunlight vs. shade) along the width of the stream at each transect, taking into account the presence or absence of vegetation. I monitored water temperature at each site year round using data loggers (StowAway TidbiT and HOBO data loggers [Onset, Pocasset, MA, USA]) as it is known to affect aquatic invertebrate species composition, life history (including timing of emergence), and production (Vannote and Sweeney 1980, Huryn and Wallace 2000). I also monitored water temperature during the summer of 2006 for the additional four sites. I measured depths and widths of the stream channels, and completed substrate surveys for each reach because the condition of the

stream bed can influence the production of algae and invertebrates (Allan 1995). At 50

locations along each reach, I randomly selected a rock, cobble, or pebble (one every 2

meters) and measured the percent it was embedded into the substrate, its size, and the

depth of water at its location (Davis et al. 2001). I analyzed % embeddedness for

particles D50 and larger. To survey potential habitat for attachment of spider webs, I

measured stream distance between vegetation over the channel and counted availability

of wood (Laeser et al. 2005).

The first biotic factor that I sampled was stream periphyton, or attached algae. To

sample periphyton, rocks were randomly selected from 5 systematically selected riffles

within each study reach and an area of 2.96 cm^2 scraped and analyzed for biomass of

chlorophyll a and ash-free dry mass. I extracted chlorophyll a following standard

methods, in 10-ml of methanol, filtered through Watman GF/F 4.7cm filters, and

estimated biomass using a spectrophotometer (model ThermoSpectronic Genesys 5)

(APHA 1995). Due to a wildfire in July 2006, which took place during the sampling

period before all periphyton samples could be collected, I substituted 2005 data for two

unburned and two low severity reaches in the analysis. Chlorophyll a data from 2005 and

2006 were compared for all sites from which data was collected in both years and no

difference in periphyton biomass between years was detected.

The biomass and composition of stream benthic invertebrates were sampled using

a Surber sampler (0.093 m^2, mesh size: 250 μm). I collected five subsamples from

random locations in systematically selected riffles (approximately every 25 meters) in

each study reach once in July 2005.

I measured the flux of adult aquatic insects emerging from each reach from May through October 2005 using 4, $0.33m^2$ floating emergence traps (Fig. 1.1, see chapter 3) set on the stream surface. Traps were placed in pools to create a good seal with the water surface as riffles experience more turbulence, and additionally because pools may be where most emergence occurs (Iwata 2006). Each set of traps accumulated insects for four to five days prior to collection, and I removed insects from the traps using an aspirator. Traps ran continuously from May through August and I collected insects from each trap every 4 or 5 days. Traps ran continuously and were sampled on a bi-weekly basis from late August through October. I sorted all benthic and adult insects and identified them to the lowest level required to classify them into trophic guilds and major life history types (usually family or genus). The latter was done mainly to address potential community compositional responses to wildfire (see chapter 2). I dried (105 °C for at least 24 hours) and weighed all insects (to nearest 0.001g) to obtain estimates of biomass for each taxon. These traps underestimate adults of bank-emerging taxa (Wallace and Anderson 1996, Stewart and Stark 2002), principally including stoneflies (Plecoptera) in these streams, which were rare in my traps. I omitted these underestimated taxa from my analyses. As insects were washed out of emergence traps during heavy rain, I considered the sample collection time to be the total days during the sampling period without rain, excluding brief rain showers.

With respect to predators of aquatic insects, I surveyed both spiders and bats. I surveyed web-weaving riparian spiders along 30-m transects encompassing both banks of each study reach during July when spiders were at peak abundance. I surveyed spiders

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by walking streams at night (22:00-00:00) when spiders were most active and visible, and recorded abundance at the family level.

I conducted surveys of bats at night at three unburned and three high severity burn sites, once in June, July, and August 2005, in conjunction with the moon phase (not during full moon). I used passive acoustic monitoring to record frequency of bat echolocation calls (AnaBat Bat Detector [Titley Electronics, New South Wales, Australia]). I did not survey low severity sites for bats due to the proximity of several of these sites to caves. Furthermore, because bats are highly mobile I could not be sure that the distance between some low severity sites and high severity habitat was great enough that bats would not forage in both habitats during a short time period. Surveys started just after dusk and were at least two hours in duration. I estimated bat foraging by counting both the number of search and feeding buzz calls. I defined a call as the start to the end of sequential pulses ending in a silent period. Because buzz calls (characterized by an increased frequency and emitted during the terminal phase of preying on an insect) were not recorded frequently, I used the combined number of buzz and search calls to estimate foraging activity, as there is a strong association between the number of search and buzz calls (Fukui et al. 2006). The silver haired bat (*Lasionycteris noctivagans*), was the dominant bat species in June while several species of *Myotis* were more common in July and August (Jason Beck, Idaho State University, *unpublished data*).

Statistical Analysis

The effect of burn severity on all habitat characteristics was analyzed using individual one-way analyses of variance (ANOVA) (PROC GLM, SAS 9.1). I tested the effect of burn severity on periphyton (chlorophyll *a* and ash-free dry mass), biomass of

benthic insects, and spider abundance using ANOVAs (PROC GLM, SAS 9.1). In the analyses of benthic insects and spider occurrence, pairwise comparisons among the least squares means for burn type were assessed using Tukey's HSD. The effect of burn severity on flux of insect emergence ($mg/m^2/day$) was analyzed using repeated measures ANOVA (PROC MIXED). Burn severity was a fixed factor and stream was a random factor in this model (stream nested within burn type). Sample periods, the unit of measurement, were repeated twenty-two times, but not all emergence traps started running at the same time in all drainages. Hence, because of missing observations some weeks, I pooled every three to four samples into six sampling periods. In the repeated measures analysis of emergence I made two *apriori* comparisons (because of low power): between unburned and high severity categories and between low and high severity categories and these were assessed using Dunnett. For the bat echolocation response, because I had only two reach types – high severity burned and unburned, I analyzed these data using a *t*-test. All biomass and count data were log-transformed to meet the assumptions of parametric analysis. Means ± one standard error are reported in the results section.

RESULTS

In general, habitat characteristics did not vary significantly among burn severity categories (Table 1.1). Potential solar insolation (from solar pathfinder), stream substrate embeddedness (Table 1.1A), distance between overhanging vegetation, and amount of wood (Table 1.1B) did not differ among burn severity categories ($F_{2,8} \leq 1.98$, $P \geq 0.200$). Despite no statistical differences in measured potential solar insolation (shading not

incorporated), there was a significant difference in photosynthetically active radiation readings at stream surfaces by burn category ($F_{2,8} = 4.02$, P=0.062). Two times greater photosynthetically active radiation reached the stream surfaces at the high severity burn vs. unburned sites (Table 1.1B; 954 ± 211 vs. 458 ± 106 µmol; Tukey HSD, $P = 0.360$), and almost seven times more reached the surface of high severity burned streams than low severity burned streams (Table 1.1B; 954 ± 211 vs. 143 ± 71 µmol; Tukey HSD, $P = 0.059$). Although there were differences in light there were no differences in water temperature, as annual degree days did not differ by burn category (Table 1.1B; $F_{2,9} = 0.83$, $P = 0.471$). The low severity burned reaches had marginally smaller median substrate size than both the unburned and high severity burn categories (Table 1.1A; 10.5 ± 3.6 vs. 20.3 ± 2.7 and 18.7 ± 2.0 cm; $F_{2,9}$=3.27, $P = 0.086$), consistent with these sites being in slightly smaller streams. The low severity burn category also had marginally smaller widths and depths, than both the unburned and high severity burn categories ($F_{2,9} \geq 2.72$, $P \leq 0.119$).

Contrary to my hypothesis I observed no difference in periphyton chlorophyll *a* ($F_{2,13} = 1.20$, $P = 0.308$) or ash-free dry mass ($F_{2,13}$ =1.17, P=0.316) among burn categories (Fig. 1.3A). Both the unburned and high severity burn sites were similar in chlorophyll *a* (Fig. 1.3A), but the low severity burn category had a slightly lower chlorophyll *a*. Both the unburned and high severity burn sites also had similar ash-free dry mass of periphyton (6.9 ± 1.2 vs. $7.5 \pm .8$ g/m^2), and the low severity category had a slightly lower ash-free dry mass (5.8 ± 1.2 g/m^2).

Although I did not observe a difference in biomass of periphyton, there was a highly significant overall effect of burn type on biomass of benthic insects ($F_{2,9} = 41.04$,

$P<0.0001$). High severity and unburned categories had a greater biomass of benthic insects than low severity categories (Fig. 1.3B). In contrast to our incremental hypothesis, the greatest difference observed was actually between high and low severity burn categories, with high severity burn sites having almost five times the biomass of benthic insects as low severity burn sites (Tukey HSD, $P < 0.0001$) and 1.6 times the biomass of benthic insects as unburned reaches (Tukey HSD, $P = 0.100$). The latter comparison was not significant due to the high variability of burned reaches versus unburned reaches (Fig. 1.3B, error bars).

The ordinal magnitude of emerging insect biomass in the three reach types was similar to that for benthos, with high severity reaches having the greatest emergence, unburned reaches falling intermediate, and low severity reaches falling the lowest (Fig. 1.3C). There was a significant overall effect of burn severity on aquatic insect emergence ($F_{2,9} = 4.03$, $P = 0.056$ by ANOVA). This analysis was based on over 700 samples collected from 22 different sample periods and 12 streams, during June through October 2005. The difference between unburned and low severity reaches was very small (Dunnett, $P=0.985$), whereas the biomass of emerging insects was more than two-fold greater from the high severity burn category than the unburned category (Dunnett, $P = 0.093$). The biomass of emerging insects was almost three-fold greater from the high severity burn category than the low severity burn category (Tukey HSD, $P = 0.036$). I also observed a significant effect of time on emergence ($F_{5,28} = 6.74$, $P = 0.0003$) with the greatest biomass difference between burn categories occurring early in the summer during peak emergence. For example, emergence was up to five-fold greater in high severity burn sites than both unburned and low severity burn sites during the month of

June. Though the biomass of emergence became more similar among burn categories by late July, this same pattern held throughout August, September and October when total emergence was lower. There was no significant interaction between time and burn type ($F_{10.28}$ = 1.26, P = 0.301).

I also observed effects of wildfire on insectivorous predators. The density of tetragnathid spiders differed by burn category, though the overall effect was only marginally significant ($F_{2,13}$ = 3.22, P=0.073). The ordinal magnitude of the three burn categories was again the same as that for benthic invertebrates and emerging insects. However, the difference was only significant between high and low severity burn reaches (Fig. 1.3D; Tukey HSD, P=0.062). No significant differences were observed between high severity and unburned categories (Tukey HSD, P=0.55) or between unburned and low severity categories (Tukey HSD, P=0.32). In terms of vertebrate predators, I detected more bats (based on echolocation calls) in high severity burned reaches than in unburned reaches (Fig. 1.3E; P = 0.04 by t-test). Greater numbers of both tetragnathid spiders and bats were observed foraging in high severity burn reaches, where emergence was measured to be the greatest.

DISCUSSION

The findings of this study are among the first to suggest that high severity wildfire may drive a substantial pulse in aquatic productivity that is, detectable at multiple trophic levels including among terrestrial consumers. I observed the greatest biomass of benthic insects and emerging adult aquatic insects, occurrence of tetragnathid spiders, and frequency of bat echolocation calls in reaches that had been severely burned (missing

both riparian vegetation and the conifer canopy) five years prior. Several studies have documented a short-term pulse of nutrients into streams after fire (Wright 1976, Tiedemann et al. 1978, Schindler et al. 1980, Spencer and Hauer 1991). I observed that the predominant effects of wildfire continue at least 5 years post-fire with an extended "fire-pulse" of productivity. Rather than the flux from land to water characteristic of short-term fire effects, this midterm increase in productivity was dominated by an increase in aquatic insects available to terrestrial predators. Just as the input of wood into streams continues for many years after a fire (Minshall et al. 1989), providing important structure for stream channels (Gregory et al. 2003), this mid-term "fire-pulse" may extend the positive effects of wildfire by fueling aquatic insect production that subsidizes terrestrial habitats. As observed by Nakano and Murakami (2001), such a subsidy could be especially important in the winter, spring, and early summer when terrestrial food resources are less available for riparian predators like spiders, bats, and birds. Though the magnitude of organic matter flux via emerging insects is very small compared to that from the land to water (Fisher and Likens 1973, Webster and Patten 1979), the quality of these prey is high and may be of disproportionate importance to terrestrial predators (Baxter et al. 2005). Just as the "flood pulse" (Junk et al. 1989) delivers terrestrial carbon to rivers and the land is subsidized by water and other materials, wildfire also results in amplified reciprocal fluxes between the land and the water and its effects extend many years after the event. Increased post-fire productivity within streams also has the potential to fuel in-stream food webs, including insect predators within the stream (see chapter 2), as well as other predators like fish (Dunham et al. 2007, Koetsier et al. 2007). Furthermore, in the Big Creek Watershed a greater export of drifting insects and

aggregation of feeding trout at confluences of burned versus unburned tributaries has been observed, suggesting that fire induced increases in productivity of tributaries might have important consequences for downstream fisheries (Patrick Della Croce and C. Baxter, *unpublished data*).

The mechanisms producing increases in benthic and emerging insects are not clear. I initially hypothesized a bottom-up effect; i.e., an increase in consumers driven by an increase in primary producers. However, I found no significant difference in periphyton despite the fact that there was a greater amount of light available at high severity burned sites. There are a number of reasons why I may not have observed differences in periphyton by burn severity category. First, I measured biomass at one point during the summer, which is often a poor indicator of actual primary production. It is possible that though similar biomass occurs, production of algae varies by burn-severity category because there is a more rapid turnover of algae at high-severity burn sites. Second, there may be greater production of algae at high severity sites, but also greater insect grazing effects that create similar biomass of periphyton in different burn categories. Third, there may have been differences among categories but our sampling method did not have sufficient power or precision to detect them. Fourth, there may not be a difference in biomass or production of algae in the midterm period following wildfire in these streams if they were limited by something other than sunlight, such as nutrients (Marcarelli and Wurtsbaugh 2007). Given the patchiness of periphyton growth in both space and time and that the pattern was similar to those I observed for higher trophic levels (just not significant), it seems likely that the reason that I did not observe a pattern in biomass of chlorophyll *a* is a combination of the three possibilities.

Another possible mechanism that could have contributed to increased aquatic insect production might be that sites that experienced high severity fire received increased inputs of allochthonous carbon. The re-growth of riparian vegetation following a fire is likely to include proportionately more herbaceous plants and deciduous shrubs and trees than might have been present pre-fire (Dwire and Kauffman 2003). Consequently, there may be greater delivery of more labile (edible) plant material to streams at burned versus unburned sites, and this material (combined with in-stream sources of detritus) may drive increased production among detritivorous stream insect larvae (Minshall 2003). However, a parallel study to this one, located on the same study streams, compared flux of allochthonous inputs between unburned and high severity burn categories, and no differences were observed (Breanne Jackson and Jeff Braatne, University of Idaho, *unpublished data*). There may be a difference in the food quality of those allochthonous inputs, but this has not been investigated.

One further mechanism could be that rather than being caused by a change in basal resources, the observed increase in insect emergence may have been driven by a compositional shift in the invertebrate community. Previous studies have shown that benthic invertebrate communities can change in composition following wildfire (Mihuc et al. 1996, Minshall et al. 1997, Minshall et al. 2001). Generalist herbivore-detritivore taxa, like *Baetis* (Baetidae) and Chironomidae have fast life histories and seem to be best adapted for the variable physical conditions found in many post-fire streams (Mihuc and Minshall 1995, Mihuc et al. 1996). As these *r*-strategists (*sensu* Pianka 1970) produce more generations per year, a greater flux of emergence could be produced from sites that experienced high severity fire due to the faster turn over of these taxa. In fact, I did

observe a greater flux of both Chironomidae and *Baetis* emerging from high severity burn sites than either unburned or low severity burn sites (see chapter 2). Thus, the difference in emergence could have been driven by a shift in community composition to include more productive taxa following wildfire, serving to stimulate the flux of adult insect emergence to terrestrial habitats.

In addition to describing a mid-term response to fire, my results also suggest that fire severity matters, and that different types of fire may not have the same impacts on stream-riparian ecosystems. Surprisingly, some of the strongest differences I observed were between the high severity and low severity burned reaches. High severity fire appeared to stimulate the production of more benthic invertebrates, greater emergence, and more spiders and bats, while low severity fire seemed to have no effect, or possibly inhibited production (low severity reaches had slightly lower values for some response variables than unburned reaches). Thus, the severity of the fire could determine both the strength and direction of the response to wildfire. However, I do not know the mechanisms behind differences I observed. The differences might simply have been the result of more sunlight entering the sites that experienced high severity versus low severity fire. Additionally, the sites that experienced low severity fire had a dense growth of riparian shrubs, reflected in greater shading and lower PAR than unburned sites, even though their upper canopies were slightly more open than unburned reaches. Yet, if differences in insect productivity were only the indirect result of increased sunlight, I might have expected to detect differences in periphyton biomass. It is also possible that the differences between the high and low severity categories are in part due to an effect of stream size as the low severity category included slightly smaller streams (Table 1.1A).

Alternatively, it is possible that high severity fire results in great enough hydrologic changes and associated streambed disturbance to shift the community to dominance by *r*-strategist taxa which results in greater emergence, whereas low severity fire may not trigger enough streambed disturbance to create such a community shift. Monitoring of some of the sites in the Big Creek watershed suggests that a major scouring event has not occurred since the 2000 fire (G.W. Minshall, *unpublished data*). Thus, there may be a threshold of disturbance frequency or intensity (Townsend 1989) that may explain differences between sites experiencing high vs. low severity fire. More studies that focus on comparing the effects of wildfire of different severities on stream-riparian ecosystems are necessary to address this possibility.

The results of this study may have implications for fire management, but the effect of fire observed may also change with land use context and forest type. It is necessary to manage wildfire with principles based on ecosystem patterns and processes, rather than an aim to simply 'control' fire (Beschta et al. 1995). In fact, my results suggest that permitting high severity fires to burn in certain forest types could be important in maintaining ecosystem function, and that low severity fires may not achieve the same results. Yet, this study was conducted in a wilderness area where streams have been very marginally impacted by humans and the linkages between streams and their surrounding riparian zones are intact. The effects of wildfire might be much different for stream-riparian areas that have been altered or where linkages have already been disconnected. The results of this study should not be extrapolated to landscapes of the western U.S. without additional work that focuses on effects of high severity wildfire in watersheds that have experienced more human-induced changes. Study of the role of

high severity fire in the context of varying land use will provide the necessary

understanding to make informed decisions regarding management of wildfire in

landscapes.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington.

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

APHA. 1995. Standard methods for the examination of water and wastewater, 18th edition. American Public Health Association, Washington, DC, USA.

Bailey, J. K., and T. G. Whitham. 2002. Interactions among fire, aspen, and elk affect insect diversity: Reversal of a community response. Ecology **83**:1701-1712.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology **85**:2656-2663.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Beschta, R. L., C. A. Frissell, R. E. Gresswell, F. R. Hauer, J. R. Karr, G. W. Minshall, D. A. Perry, and J. J. Rhodes. 1995. Wildfire and Salvage Logging: Recommendations for Ecologically Sound Post-Fire Salvage Logging and Other Post-Fire Treatments on Federal Lanes in the West. (26 November 2007; www.saveamericasforests.org/congress/Fire/Beschta-report.htm).

Bisson, P. A., D. R. Montgomery, and J. M. Buffington. 2006. Valley segments, stream reaches, and channel units. Pages 23-49 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology. Academic Press, San Diego.

Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessberg, D. C. Lee, J. L. Kersner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management **178**:213-229.

Collier, K. J., S. Bury, and M. Hibbs. 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biology **47**:1651-1659.

Davis, J. C., G. W. Minshall, C. T. Robinson, and P. Landres. 2001. Monitoring wilderness stream ecosystems. General Technical Report RMRS-GTR-70, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Laeser, S. L., C. V. Baxter, and K. D. Fausch. 2005. Riparian vegetation loss, stream channelization and web-weaving spiders in northern Japan. Ecological Research **20**:646-651.

Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. BioScience **24**:447-456.

Malison, R. L. 2008a. The design and use of a light-weight floating emergence trap. M.S. Thesis Chapter 3. Idaho State University, Pocatello.

Malison, R. L. 2008b. Streams affected by wildfire of varying severity differ in aquatic insect assemblage structure and emergence. M.S. Thesis Chapter 2. Idaho State University, Pocatello.

Marcarelli, A. M., and W. A. Wurtsbaugh. 2007. Effects of upstream lakes and nutrient limitation on periphytic biomass and nitrogen fixation in oligotrophic, subalpine streams. Freshwater Biology **52**:2211-2225.

Mihuc, T. B., and G. W. Minshall. 1995. Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. Ecology **76**:2361-2372.

Mihuc, T. B., G. W. Minshall, and C. T. Robinson. 1996. Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. Pages 83-94 *in* J. M. E. In: Greenlee, editor. Ecological Implications of Fire in Greater Yellowstone. International Association of Wildland Fire.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology **48**:139-149.

Minshall, G. W. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management **178**:155-161.

Minshall, G. W., J. T. Brock, D. A. Andrews, and C. T. Robinson. 2001a. Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. International Journal of Wildland Fire **10**:185-199.

Minshall, G. W., J. T. Brock, and J. D. Varley. 1989. Wildfire and Yellowstone's stream ecosystems. BioScience **39**:707-715.

Minshall, G. W., C. T. Robinson, and D. E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences **54**:2509-2525.

Minshall, G. W., C. T. Robinson, D. E. Lawrence, D. A. Andrews, and J. T. Brock. 2001b. Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbances by wildfire. International Journal of Wildland Fire **10**:201-213.

Minshall, G. W., T. V. Royer, and C. T. Robinson. 2004. Stream ecosystem responses following the Yellowstone wildfires: the first 10 years. Pages 87-97 *in* L. Wallace, editor. After the fires: the ecology of change in Yellowstone National Park. Yale University Press, New Haven, CT.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology **80**:2435-2441.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America **98**:166-170.

Paetzold, A., C. J. Schubert, and K. Tockner. 2005. Aquatic-terrestrial linkages along a braided river: riparian arthropods feeding on aquatic insects. Ecosystems **8**:748-759.

Pianka, E. R. 1970. On r- and K-selection. The American Naturalist **104**:592-597.

Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291-314 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. Ecological consequences of habitat heterogeneity. Blackwell Scientific, Oxford, UK.

Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K. Marsee, and C. Anderson. 2004. River to watershed subsidies in an old-growth conifer forest. Pages 217-240 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago, IL, U.S.A.

Robinson, C. T., S. R. Rushforth, and G. W. Minshall. 1994. Diatom assemblages of streams influenced by wildfire. Journal of Phycology **30**:209-216.

Schindler, D. W., R. W. Newbury, K. G. Beaty, J. Prokopovich, T. Ruszczynski, and J. A. Dalton. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Canadian Journal of Fisheries and Aquatic Sciences **37**:328-334.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications **6**:185-199.

Spencer, C. N., and F. R. Hauer. 1991. Phosphorous and nitrogen dynamics in streams during wildfire. Journal of the North American Benthological Society 10:24-30.

Stewart, W. S., and B. P. Stark. 2002. Nymphs of North American Stonefly Genera (Plecoptera), Second edition. The Caddis Press, Columbus, OH.

Tiedemann, A. R., J. D. Helvey, and T. D. Anderson. 1978. Stream chemistry and watershed nutrient economy following wildfire and fertilization in Eastern Washington. Journal of Environmental Quality 7:580-588.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36-50.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411-433.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. The American Naturalist 115:667-695.

Wallace, J. B., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-86 in R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. Science 313:940-943.

Williams, D. D., L. G. Ambrose, and L. N. Browning. 1995. Trophic dynamics of two sympatric species of riparian spider (Araneae: Tetragnathidae). Canadian Journal of Zoology 73:1543-1553.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 54:1259-1269.

Wright, R. F. 1976. The impact of forest fire on the nutrient influxes to small lakes in northeastern Minnesota. Ecology 57:649-663.
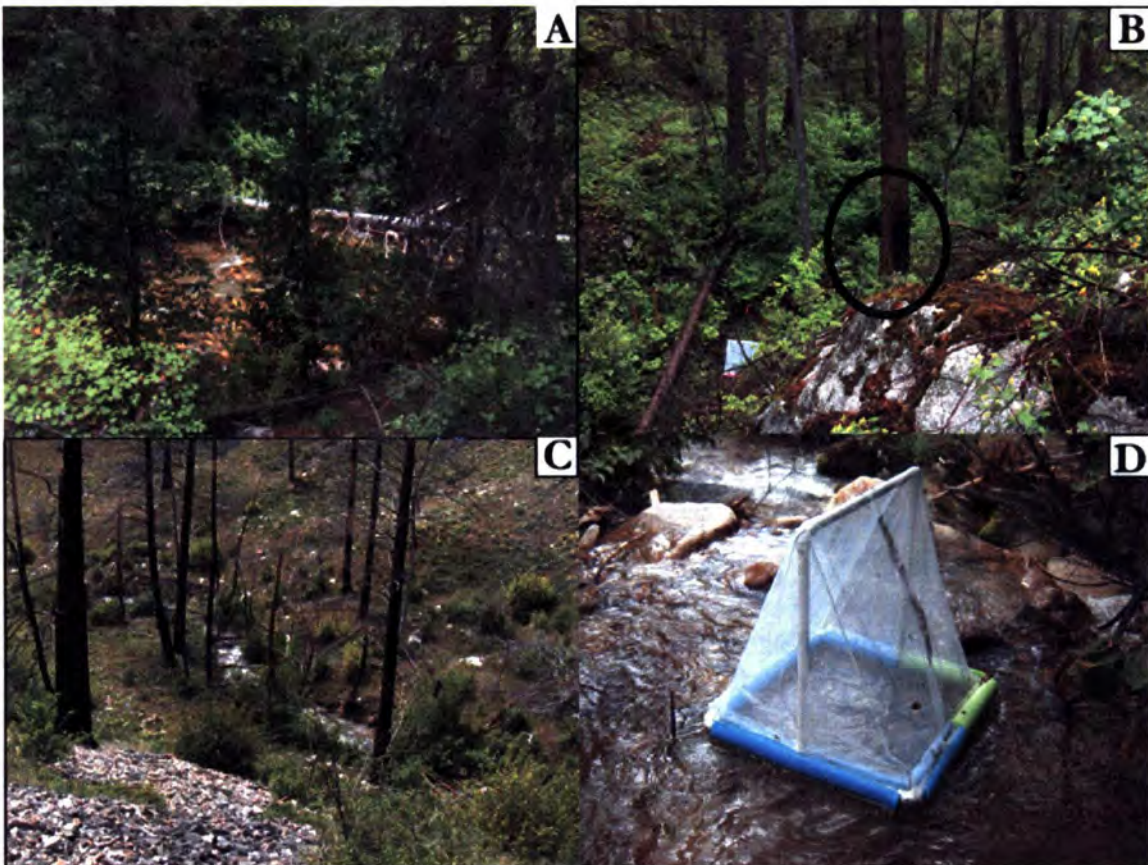
Figure 1.1. Pictures of the three fire classes determined based upon existing post-fire vegetation in 2005: A – Unburned, within the last 50 years; B – Low Severity Burn, where fire burned riparian vegetation (as evidenced by circled fire scar), but canopy remained intact; and C – High Severity Burn, with both riparian vegetation burned and canopy removed by wildfire. D – Example of floating emergence trap used to collect emerging aquatic insects.
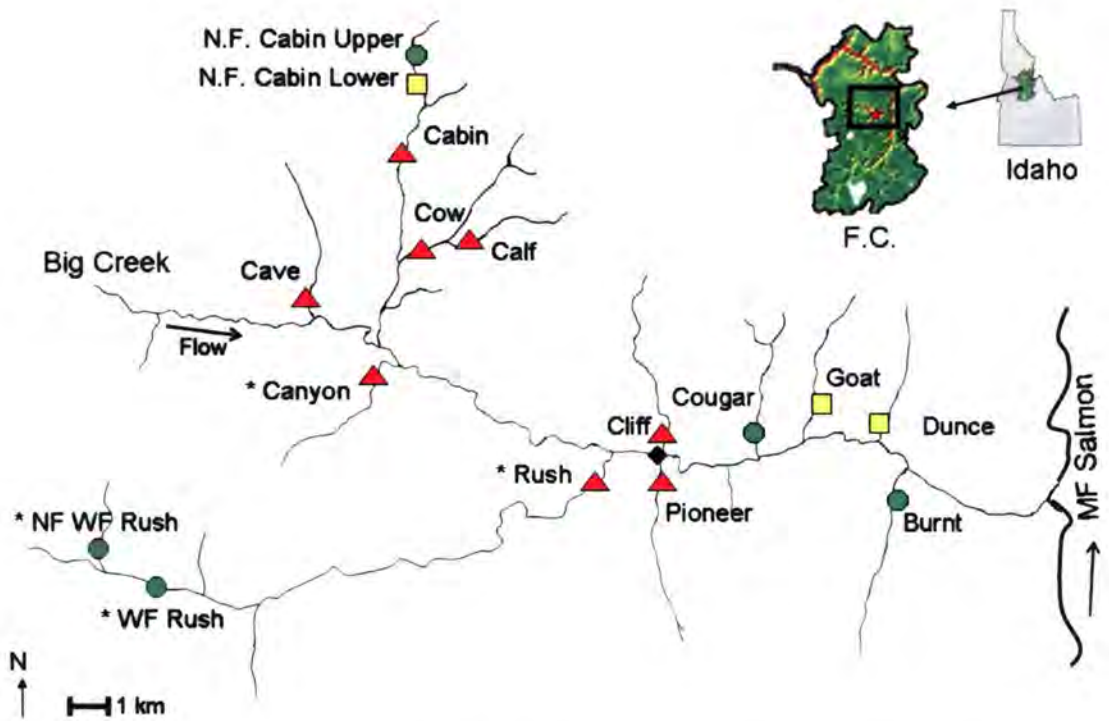
Figure 1.2. Study reaches in the Big Creek Watershed, located in the Frank Church 'River of No Return' Wilderness Area in central Idaho. Reaches are all located on tributaries of Big Creek which flows into the Middle Fork of the Salmon River. Twelve reaches were studied in 2005, and four additional reaches were sampled during 2006, marked with asterisks. Circles represent unburned sites (n = 5), squares low severity burn sites (n=3), and triangles high severity burned sites (n=8). The diamond marks the location of Taylor Ranch Wilderness Field Station.
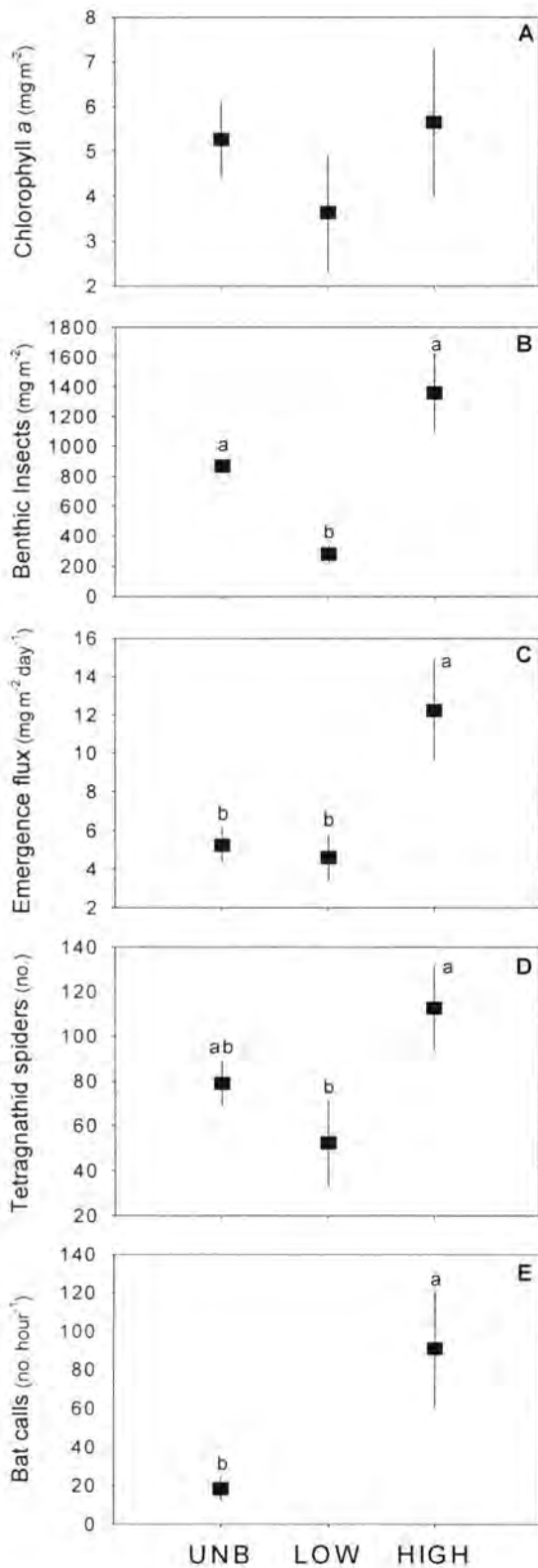
Figure 1.3. Results of five food web components sampled in 2005: A – Periphyton chlorophyll *a*, B – Biomass of Benthic Insects, C – Emergence Flux, D – Number of Tetragnathid Spiders, and E – Number of Bat Echolocation Calls, in reaches of three fire classes [UNB = unburned (n=5 for chlorophyll a and spiders, n=3 for benthic invertebrates, emergence and bats), LOW = low severity burn (n=3 for chlorophyll a, benthic invertebrates, emergence and spiders), HIGH = high severity burn (n=8 for chlorophyll a and spiders, n=6 for benthic invertebrates and emergence, n=3 for bats)]. Different letters indicate significant differences (*P*<0.05) among burn types based on LSD comparisons after ANOVA of log-transformed data. However, differences indicated in number of Tetragnathid spiders and between high severity and unburned emergence were marginally significant (*P*=0.07 and 0.09, respectively).

TABLES

Table 1.1A. Physical habitat parameters measured for study sites. Sites marked with asterisks (NFWF Rush, WF Rush, Canyon, and Rush) were added in 2006 for collection of additional periphyton samples and spider surveys. Means ± 1 standard deviation are reported, except standard errors are reported for depth. Double asterisk indicates missing data point.

	Site Characteristics						
	Width (m)	Depth (m)	Substrate Size (cm)	Embeddedness (% embedded)	Aspect	Slope (%)	Elevation (m)
Unburned							
Burnt	2.82 ± 0.38	0.13 ± 0.02	24.8 ± 20.1	47 ± 39	N	**	1300
Cougar	2.14 ± 0.67	0.19 ± 0.01	20.7 ± 27.9	34 ± 28	S	12	1180
NF Cabin Upper	1.18 ± 0.40	0.11 ± 0.01	15.4 ± 23.9	46 ± 23	S	18	1601
NFWF Rush*	0.82 ± 0.28	0.06 ± 0.01	12.1 ± 17.8	55 ± 31	S	8	1642
WF Rush*	2.20 ± 1.14	0.1 ± 0.01	10.3 ± 14.8	33 ± 23	E	5	1623
Low Severity							
Dunce	1.15 ± 0.44	0.11 ± 0.02	16.1 ± 32.3	56 ± 21	S	26	1165
Goat	0.8 ± 0.28	0.12 ± 0.01	3.9 ± 10.0	47 ± 28	S	7	1328
NF Cabin Lower	1.43 ± 0.29	0.11 ± 0.01	11.4 ± 23.8	48 ± 28	S	14	1584
High Severity							
Cabin	3.74 ± 1.16	0.24 ± 0.02	20.3 ± 17.8	50 ± 36	S	5	1406
Calf	0.92 ± 0.29	0.09 ± 0.01	21.1 ± 33.7	47 ± 37	SW	14	1394
Canyon*	2.13 ± 0.44	0.12 ± 0.02	13.0 ± 18.5	39 ± 33	N	9	1267
Cave	4.08 ± 0.99	0.21 ± 0.01	14.0 ± 16.9	37 ± 35	S	6	1238
Cliff	3.11 ± 0.86	0.24 ± 0.02	19.6 ± 16.5	22 ± 33	S	13	1213
Cow	1.85 ± 0.41	0.16 ± 0.01	25.5 ± 24.4	46 ± 30	SW	13	1373
Pioneer	2.68 ± 0.56	0.20 ± 0.01	11.8 ± 20.2	26 ± 28	N	10	1248
Rush*	10.6 ± 1.65	0.33 ± 0.01	15.6 ± 16.8	41 ± 27	N	2	1182

Table 1.1B. Physical habitat parameters measured in streams of the Big Creek Watershed in 2005 and 2006, including annual degree days, photosynthetic active radiation (PAR), solar insolation, canopy cover, and distance between overhanging vegetation and number of pieces of wood (for spider web attachment). Asterisks mark sites added in 2006 for collection of additional periphyton samples and spider surveys. Double asterisks indicate data not collected due to logistical constraints. Cabin Creek degree days are based on only October 20, 2005 through July 19, 2006 (10 months) due to a missing data logger. Means ± 1 standard deviation are reported.

	Site Characteristics					
	Annual degree days	PAR (µmol)	Solar insolation	Canopy cover (%)	Distance between vegetation (m)	Wood count (# of pieces)
Unburned						
Burnt	1993	**	**	96.75	**	**
Cougar	2126	564 ± 689	1435 ± 133	97.99	0.51 ± 0.76	22.1 ± 13.0
NF Cabin Upper	1649	351 ± 545	1272 ± 27	97.60	0.35 ± 0.49	7.3 ± 7.1
NFWF Rush*	**	105 ± 211	1362 ± 69	67.44	0.0 ± 0.0	14.8. ± 12.6
WF Rush*	**	713 ± 908	1356 ± 44	73.68	0.37 ± 0.70	19.4 ± 19.1
Low Severity						
Dunce	3144	107 ± 190	1107 ± 142	94.87	0.0 ± 0.0	23.5 ± 14.1
Goat	2041	42 ± 121	1452 ± 33	91.42	0.0 ± 0.0	35.3 ± 10.4
NF Cabin Lower	1819	281 ± 391	1358 ± 26	91.94	0.29 ± 0.40	23.1 ± 15.0
High Severity						
Cabin	955***	1417 ± 849	1311 ± 35	78.81	2.25 ± 1.43	36.3 ± 19.2
Calf	2059	99 ± 274	1130 ± 73	64.06	0.05 ± 0.15	4.9 ± 3.3
Canyon*	**	**	1195 ± 38	25.51	0.46 ± 0.44	16.7 ± 12.7
Cave	2271	1184 ± 743	1361 ± 18	42.41	3.35 ± 1.63	40.5 ± 21.0
Cliff	2427	1463 ± 743	1381 ± 18	53.79	1.71 ± 0.89	19.8 ± 12.5
Cow	2241	679 ± 794	1319 ± 23	68.09	0.67 ± 0.60	20.2 ± 12.6
Pioneer	1937	881 ± 716	1248 ± 24	83.62	0.44 ± 0.88	11.8 ± 6.8
Rush*	**	1942 ± 107	1408 ± 36	20.12	8.96 ± 2.15	20.4 ± 8.4

CHAPTER 2

WILDFIRE OF VARYING SEVERITY AFFECTS THE EMERGENCE AND STRUCTURE OF AQUATIC INSECT ASSEMBLAGES

INTRODUCTION

Wildfire may cause disturbance that alters stream insect assemblages. Streams and aquatic insects are affected by wildfire in the short, mid, and long-term time periods. Direct, immediate effects of fire on aquatic insects are often negligible, but exceptions include intense heating of water, long exposure to smoke, and more often the replacement of food resources with ash and charcoal, leading to increased mortality of aquatic insects, especially over winter (Minshall 2003). Indirectly, the greatest effect of fire on aquatic insect assemblage structure may result from disturbance by flooding and/or mass sediment movements during the spring runoff of the years following fire (Minshall 2003). Increased runoff creates open patches on the stream bed as insects are scoured from the substrate (Resh et al. 1988, Lake 2000), and these disturbed habitats can then be recolonized, potentially changing the aquatic insect assemblage. In some cases, post-fire sedimentation may reduce the quality of habitat available to aquatic insects, which could either delay recolonization, or allow only a small component of the insect assemblage to be successful in the newly disturbed habitat. Shifts in the colonization of insects post-disturbance are well documented (Townsend and Hildrew 1976, Clements et al. 1989, Moser and Minshall 1996). For instance, Miyake et al. (2003) found that mobile taxa, such as *Baetis* (Ephemeroptera), are more successful colonizers following flood disturbance. Good colonizers are often also trophic generalists, and may be disturbance-adapted (Mihuc and Minshall 1995). Thus, taxa like *Baetis* may be favored over others

in streams following wildfire (Mihuc et al. 1996). Furthermore, these disturbance adapted trophic generalists often exhibit r-selected (*sensu* Pianka 1970) life histories, with short generation times, high fecundity, and high dispersal rates compared to other taxa.

An assemblage shift after fire to more disturbance-adapted, r-strategist primary consumers may result in increased insect production, including increased emergence of adult aquatic insects. Although several studies have investigated the effects of wildfire on insect assemblage structure (Mihuc et al. 1996, Minshall et al. 1997, Minshall 2003), none have estimated the response of aquatic insect production to disturbance by wildfire. Such an increase in the productivity of primary consumers may propagate up the food chain to insect predators within the stream, as well as to terrestrial predators that feed on emerging adult insects (see chapter 1). Following wildfire, production of predatory aquatic insects within the stream may increase with additional food resources, especially if such predators specialize in preying on disturbance-adapted primary consumers. This effect would be even stronger if the predators were capable of producing multiple generations per year under good conditions. However the hypothesis that fire may drive increased production of primary and secondary consumers has not been evaluated.

The effects of disturbance, like wildfire, on aquatic insect assemblages and aquatic insect production can be evaluated by study of both the benthic larval stage and emergence of adult insects. Benthic samples, usually collected during summer low-flow periods, have traditionally been used to study insect assemblages in streams. Though this type of sampling can be used to accurately assess the abundance of most taxa present at a site, this technique does not provide an integrated perspective over the time frame of

insect life cycles. There is a strong relationship between the biomass of emerging adult insects and benthic insect secondary production (measured by growth or cohort techniques), and emergence samples are a good indicator of total benthic insect production (Statzner and Resh 1993, Benke and Huryn 2006). Emergence data provide a temporal perspective of the dynamics and productivity of the insect assemblage. Emergence traps may also capture insects that might be missed in benthos samples which are typically taken from riffle habitats. Thus, measurement of emergence provides a set of community data complementary to that from sampling the benthos.

The response of stream insect assemblage diversity to effects of fires of varying severity has not been evaluated. Fire severity can vary considerably from complete canopy removal, to ground fires whose effects may barely be visible only years later. Increased disturbance and productivity may affect species diversity, and the greatest response may be found at intermediate levels (Connell 1978, Tilman and Pacala 1993, Abrams 1995). Findings differ as to whether intermediate levels of disturbance (i.e. intermediate frequency and intensity of flooding) produce the highest level of diversity in stream systems. Some studies have failed to detect important effects of disturbance on aquatic insect species diversity (Robinson and Minshall 1986, Death and Winterbourn 1995) while others have found support for the intermediate disturbance hypothesis (Ward and Stanford 1983, Townsend and Scarsbrook 1997, Miyake and Nakano 2002). There is a need to investigate the effects of different severities of wildfire on species diversity and productivity to understand how varying intensities of fire differ in their disturbance of aquatic habitats over time.

Most studies of the effects of wildfire on stream ecosystems have focused on the immediate or short-term time period following a fire. However, the effects of wildfire on stream systems vary with time after a fire. Minshall et al. (2004) categorized four stages of watershed response and recovery following fire as: (1) immediate (the time of active burning to a few days after), (2) short-term (a few days to the beginning of spring run-off), (3) mid-term (usually from spring runoff of the 1st post-fire year to sometime beyond the 10th year), and (4) long-term (occurring decades or centuries later). Studies of aquatic insects have focused on the immediate and short term time periods following disturbance, and there is a lack of understanding as to what degree and for how long fire effects extend post-fire. Thus, there is a need for investigations of the effects of wildfire on stream insect assemblage composition and productivity in the mid-term time period.

Here I report results from a comparative study that examined the mid-term effects of wildfire of varying severity on insect assemblage composition and emergence. I hypothesized that wildfire would alter the structure of the aquatic insect assemblage, resulting in greater production of insect consumers and predators. To investigae this hypothesis I compared benthos and emergence data in a suite of unburned watersheds to those that had experience low-severity and high-severity wildfire. I tested four predictions: (a) sites that experienced wildfire will have greater biomass of aquatic insect primary consumers, primarily due to higher abundance of r-strategist taxa, (b) greater biomass of prey will be associated with increased production of insect predators at burned vs. unburned sites, (c) sites that burned with high-severity will have the most disturbed substrate, unburned sites will have the least disturbed substrate, and low severity sites will fall intermediate, and (d) that sites that burned with low-severity will

have the greatest insect species richness. Because of the benefits inherent in both benthic and emergence sampling methods, I used both types of data in this study.

METHODS

Study Site

Study streams were located within the Payette National Forest in central Idaho. Reaches were located on tributaries of Big Creek, which flows into the Middle Fork of the Salmon River in the Frank Church 'River of No Return' Wilderness Area. The streams flow through steep, narrow valleys with forested slopes of primarily Douglas-Fir (*Pseudotsuga menziesii*) and/or Ponderosa Pine (*Pinus ponderosa*). Also present are extensive bare or sparsely vegetated areas and open areas of grass and sagebrush (*Artemisia*) are also common on the drier slopes. Dominant riparian vegetation includes Red Osier Dogwood (*Cornus sericea*), Rocky Mountain Maple (*Acer glabrum*) and Alder (*Alnus viridis*). The landscape generally receives between 38-50 cm of precipitation in the valleys and 76-100 cm at higher elevations, the majority of which occurs as snow, resulting in peak flows from late spring through early-summer (Robinson et al. 2005). The streams generally remain at baseflow conditions from late summer through winter. I chose to study the effects of wildfire in this wilderness watershed because I wanted to measure responses by stream ecosystems mostly unaltered by humans, and also because here natural fire regimes have been minimally affected by fire suppression or land cover change. The Big Creek drainage experienced an intense wildfire in 2000 (the Diamond Fire) which burned most of the lower portion of the Big Creek drainage. This area has also been affected to varying degrees by other fires, including the Golden Fire of 1988, the Rush Point Fire of 1991, and the Dunce Fire of 2006.

I selected study streams that were affected by the 2000 Diamond fire to varying

degrees. Based upon the condition of the post-fire riparian vegetation in 2005, I

categorized reaches in tributaries of the lower Big Creek drainage into three classes: (1)

'high severity burn,' where wildfire removed both riparian understory and canopy, and

presently only the understory has returned; (2) 'low severity burn,' where fire removed

the understory but not canopy, and the understory has returned under an intact canopy;

and (3) 'unburned,' where the reach was entirely unburned or burned long ago (>50

years). Due to the spatial extent and high severity of the Diamond fire, my study was

unbalanced, with six high severity reaches, three low severity reaches, and three

unburned reaches. Six high severity sites were selected to increase statistical power, as it

was impossible to find additional unburned and low severity study reaches close enough

to the study area for repeated sampling. Within these classifications I selected 100 m

study reaches and used segment and reach classification (*sensu* Frissell et al. 1986,

Bisson et al. 2006) to identify sites that were similar in stream size, valley segment type,

and reach type. All were 2nd-3rd order streams, in alluvial valley segments and step-pool

reach types (Bisson et al. 2006). In addition, sites were located in the lower portion of

each tributary to facilitate access via hiking.

Sampling

I measured the biomass, number, and composition of benthic insects and

emerging aquatic insects, along with various physical habitat parameters from all study

reaches. At each site, I collected data on a suite of physical and biological parameters

following methods of long-term studies in this area by Minshall and colleagues (see

Davis et al. 2001).

I sampled the biomass, number, and composition of both benthic and emergent stream insects. I used a Surber sampler (0.093 m^2) to sample benthic insects and collected five replicates from random locations within riffles every ~25m in the study reach, once in July 2005. I measured the flux of adult aquatic insects emerging from each reach from May through October 2005, as this is the period of the year during which the greatest emergence occurs, using four 0.33m^2 floating emergence traps (see chapter 3) set on the stream surface. Traps were placed over pools to create a good seal with the water surface as riffles experience more turbulence and additionally because pools may be where most emergence occurs (Iwata 2007). I removed insects from the traps using an aspirator. Traps were deployed continuously and each set of traps accumulated insects for 4-5 days prior to collection from May-August. Bi-weekly sampling took place from late August through October. I sorted, enumerated, and identified all benthic insects and adult insects to the lowest level (usually genus or species for benthos, and family or genus for emergence) required to address the hypotheses above. I then dried and weighed all insects (to nearest 0.001g) to obtain estimates of biomass for each taxa. These traps underestimate adults of bank-emerging taxa (Wallace and Anderson 1996, Stewart and Stark 2002), principally including stoneflies (Plecoptera) in these streams, which were rare in my traps. I omitted these underestimated taxa from my analyses. As insects were washed out of emergence traps during heavy rain, I considered the sample collection time to be the total days during the sampling period without rain, excluding brief rain showers.

At each site, I measured a range of habitat factors of potential importance to structure and productivity of aquatic insect communities. In addition to aspect, elevation, and gradient, I measured factors likely to be influenced by wildfire such as solar

radiation, temperature, stream width and depth, and streambed conditions. Increases in solar energy affect primary production and thereby alter resources for aquatic insects. In addition, I took 20 measures of PAR (Light meter [LI-COR, Lincoln, NE, USA]) (every 2 meters) starting at the beginning of each reach, just above the water surface. I took the measurement within the dominant type of light present (i.e. direct sunlight vs. shade) along the width of the stream at each transect, taking into account the presence or absence of vegetation. I measured water temperature at each site because it is known to affect aquatic insect species composition, life history (including timing of emergence), and production (Vannote and Sweeney 1980, Huryn and Wallace 2000). Temperature was monitored year-round (StowAway TidbiT and HOBO data loggers [Onset, Pocasset, MA, USA]) and summarized by annual degree days. I measured stream width and depth in all habitat types (i.e. pools vs. riffles) present within each reach. I completed substrate surveys for each reach because stream bed character is known to influence insect assemblage structure (Minshall 1984). At fifty locations along each study reach a rock was randomly selected (one every 2 meters), its size measured and its % embeddedness estimated. Percent embeddedness served as an index of degree of disturbance for benthic stream habitat to address hypothesis c, and was analyzed for particles D50 and larger.

Statistical Analysis
I used multivariate techniques to identify possible patterns in insect taxonomic composition among burn categories. I analyzed aquatic insect assemblage data by using nonmetric multidimensional scaling (Kruskal and Wish 1978) to evaluate differences among sites visually, based on separation or overlap among sites of different burn severity categories in insect assemblage space. The NMDS ordination method is well

suited to ecological data that are non-normal or discontinuous. I used biomass data for ordination of benthic insect samples because the focus of my community level analysis was to see which taxa contributed most greatly to differences in production and biomass data reflect production better than do abundance values. Relative biomass or flux (in the case of emergence) values for taxa were used for all NMDS ordinations due to high variation in raw biomass and flux values. I excluded rare taxa (less than 5 percent frequency of occurrence) from the data set (Gauch 1982) so the ordination would not be skewed by them. I used Multi-response Permutation Procedures (MRPP) to test for significant differences in community composition by burn category (Mielke and Berry 2001).

To address the hypotheses stated above and evaluate patterns detected via ordination, I tested the effect of burn severity on biomass and numbers of individual benthic insect taxa including *r*-strategist consumers, Baetis, Chironomidae, Simuliidae, and predators, *Rhyacophila*, and Tipulidae using ANOVA (PROC GLM, SAS 9.1). In the analyses of benthic insects, pairwise comparisons among the least squares means by burn type were assessed using Tukey's HSD. The effect of burn severity on emergence ($mg\,m^{-2}\,day^{-1}$) of *Baetis*, Chironomidae, Simulidae, *Rhyacophila*, and Tipulidae was analyzed using repeated measures ANOVA (PROC MIXED). Burn severity was a fixed factor and stream was a random factor in this analysis, with stream nested within burn type. Sample, the unit of measurement, was repeated twenty-two times, but not all emergence traps started running at the same time in all drainages. Hence, because of missing observations some weeks, I pooled every 3-4 samples into 6 sampling periods over the season. In the repeated measures analysis of emergence I made one *apriori*

comparison (because of low power): between low and high severity categories. Two post-hoc pairwise comparisons among least squares means for burn type were assessed using Dunnett: between unburned and low severity and between unburned and high severity categories. All biomass and count data were log-transformed to meet the assumptions of parametric analysis. For some specific hypotheses both biomass and abundance data from benthic insect samples were analyzed in order to determine whether differences were due to variation in numbers or size of individuals. The same ANOVA (PROC MIXED) test used for biomass of benthic insects was used to assess differences in insect assemblage metrics: richness and Simpson's Diversity Index. The effect of burn severity on the habitat characters I measured was analyzed using ANOVA (PROC GLM). Throughout the results, all reported values are means $\pm$ 1 standard error. Significance was assessed at the $P=0.05$ level.

RESULTS

Insect Assemblage Structure
I recently reported significant differences in total benthic biomass and overall flux of emergence by burn severity category (see chapter 1). A greater biomass of benthic insects was present and more insects emerged from high severity burn reaches versus both unburned and low severity reaches. The possible mechanisms and taxa-specific differences behind the variation by burn type are my focus here. I found no significant overall effect of burn type on species richness ($F_{2,9} = 2.40$, $P=0.146$). Species richness was similar for unburned and high severity burn categories (48.1 ± 0.9 vs. 46.1 ± 2.9 taxa, Dunnett, $P=0.867$). However, low-severity burned streams had marginally lower species richness than the high severity and unburned categories (46.1 ± 2.9 vs. 37.3 ± 4.7

taxa in high vs. low severity categories, Tukey HSD, $P=0.093$; and 48.1 ± 0.9 vs. 37.3 ± 4.7 taxa in unburned vs. low severity categories, Dunnett, $P=0.128$). There was no significant effect of burn type on Simpson's Diversity Index ($F_{2,9} = 0.79$, $P=0.484$).

In addition to differences in the overall biomass of insects, burn severity categories also differed in insect assemblage composition. A NMDS ordination of the stream mean of all benthos samples collected in 2005, based on the relative biomasses of 124 taxa, yielded a solution that represented 77% of the total variation among samples (Fig. 2.1). Burn severity categories were significantly separated in community ordination space ($A=0.096$, $P=0.002$ by MRPP). Burn severity categories separated along Axis 1, which explained 58% of the variation in the assemblage structure. Differences were most strongly driven by Ephemeroptera: Leptophlebiidae and *Baetis*, Plecoptera: Chloroperlidae and Leuctridae, Trichoptera: *Neophylax rickori*, and Diptera: *Rhabdomastix*, *Dixa*, Ceratopogonidae, *Hemerodromia*, and Chironomidae (Fig. 2.1; r-values ranging from -0.77 to -0.52 and from 0.59 to 0.76).

The overall composition of insect emergence also differed by burn severity category, but not as clearly as did the assemblage data from benthos samples. An ordination of the mean emergence for each stream from samples collected between June and October 2005, based on the relative abundance of 54 taxa, yielded a solution that represented 80% of the total variation among samples (Fig. 2.2). Burn severity categories were not significantly separated in community ordination space ($A=0.036$, $P=0.193$ by MRPP), but generally separated along Axis 1, which explained 28% of the variation in the assemblage structure. Differences were most strongly driven by Ephemeroptera: *Diphetor* and *Epeorus*, Trichoptera: *Rhyacophila vao* and *Rhyacophila sp.*, and Diptera:

Chironomidae and *Trichlinocera*, (Fig. 2.2; r-values ranging from -0.75 to -0.57 and 0.55 to 0.76). Although burn severity categories did separate in ordination space, not all sites separated into their respective categories and a clear pattern was not present due to the large amount of both spatial and temporal variation in emergence as compared to the one-time sample of benthic insect biomass and composition.

Differences in insect emergence between burn severity categories were clearer when evaluated by time period, rather than by combining many samples and multiple seasons into a single ordination. In general, throughout 2005 high severity reaches had the greatest emergence, low severity reaches had the least emergence, and unburned sites fell intermediate (Fig. 2.3). However, there was strong variation in emergence over time, with the greatest differences in emergence between burn categories occurring between the beginning of June and mid-July when emergence (at high severity sites) was most elevated (Fig. 2.3). The pulse of emergence at high severity sites during this early period was comprised largely of the following adult aquatic insects: Ephemeroptera: Heptageniidae and *Baetis*, Trichoptera: Limniphilidae, Hydropsychidae, and *Rhyacophila*, and Diptera: Chironomidae, Simuliidae, and Tipulidae. Caddisflies of the family Glossosomatidae contributed to the peak of emergence from high severity sites but also contributed to a majority of the emergence from unburned sites. Emergence by caddisflies of the family Uenoidae was not as large in magnitude but did contribute to elevated emergence in the early period. Although the greatest differences in emergence between burn severity categories occurred in the early period, the continued emergence of Chironomidae, *Rhyacophila*, and Uenoidae taxa kept emergence levels from high

severity sites elevated over levels of emergence from both unburned and low severity sites throughout summer and into the fall.

r-Strategist Primary Consumers

Baetis, Chironomidae, and Simuliidae were primarily responsible for the differences in total biomass and assemblage composition by burn category in both the benthic and emergence data. Larval biomass of these taxa was up to 18 times greater in high severity vs. unburned categories and up to 25 times greater larval biomass in high vs. low severity categories. A significant effect of burn type on biomass of *Baetis* was observed ($F_{2,9}$ = 23.78, P=0.0003). The mean biomass of larval *Baetis* was 9 times greater in the high severity vs. unburned reaches (Fig. 2.4B; Dunnett, P=0.002) and was over 25 times greater in the high vs. low severity burn reaches (Fig. 2.4B; Tukey HSD, P=0.0001). Unburned reaches also had a greater biomass of larval *Baetis* than those in the low severity category, but this difference was not significant (Dunnett, P = 0.248). The pattern for numbers of larval *Baetis* was similar to that for biomass, with a significant difference by burn type ($F_{2,9}$ = 7.31, P=0.013) driven mainly by differences between the high and low severity categories (273 ± 76 vs. 21 ± 7 ind., Tukey HSD, P=0.004). As was the case for benthos, there was also a significant effect of burn type on emergence of adult *Baetis* (Fig 2.5E; $F_{2,9}$ = 16.85, P=0.0009). A significantly greater biomass of *Baetis* emerged throughout the study period from high severity vs. both unburned and low severity sites (Fig 5E; 0.71 ± 0.26 vs. 0.10 ± 0.05 mg/m^2/day in high severity vs. unburned reaches, Dunnett, P=0.014; and 0.71 ± 0.26 vs. 0.04 ± 0.02 mg/m^2/day in high vs. low severity reaches, Tukey HSD, P= 0.0003). Slightly more biomass of *Baetis* emerged from unburned vs. low severity burn reaches (Fig 2.5E; 0.10

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± 0.05 vs. 0.04 ± 0.02 mg/m^2/day, Dunnett, P=0.171) though this difference was not significant. There was a significant effect of time on emergence of *Baetis* ($F_{5,28}$ = 6.03, P=0.0007) with their greatest emergence occurring from high severity sites between early June and late July. There was no significant interaction between time and burn type for *Baetis* ($F_{10,28}$ = 0.68, P=0.73).

Chironomidae contributed a greater biomass by burn type to both benthic and emergence samples, though the differences were mostly non-significant. There was no overall effect of burn type benthic biomass of Chironomidae ($F_{2,9}$ = 1.64, P=0.247). Though the mean benthic biomass of Chironomidae was more than 4 times greater in the high severity vs. unburned sites, this difference was not significant (Fig. 2.4B; Dunnett, P =0.769). High severity reaches had almost 17 times greater biomass of larval Chironomidae than low severity sites (Fig. 2.4B; Tukey HSD, P =0.103), but this difference was marginally significant due to high variation. There was no difference in biomass of larval Chironomidae between unburned and low severity categories (Fig. 2.4B; Dunnett, P=0.487). Although there were no statistically significant differences in number of larval Chironomidae by burn type, the pattern was similar to that for Chironomidae biomass ($F_{2,9}$= 1.20, P=0.345). Though the overall effect of burn type on emergence of Chironomidae was not significant (Fig 2.5D; $F_{2,9}$ = 1.03, P=0.397), greater biomass of Chironomidae did emerge from high vs. low severity burn categories (Fig 2.5D; 1.48 ± 0.34 vs. 0.38 ± 0.1 mg/m^2/day, Tukey HSD, P=0.187). There was a significant effect of time on emergence of Chironomidae ($F_{5,28}$ = 5.19, P=0.002) with the most occurring between early June and late July for the unburned category, while emergence peaked at high severity sites both between June 27th and July 10th and again in

late August and throughout early September. The greatest difference in Chironomidae emergence by burn type occurred at the end of the sampling period when overall emergence was low but still elevated from reaches in the high severity category as compared to those in both the unburned and low severity categories. There was no significant interaction between time and burn type for Chironomidae ($F_{10,28} = 0.91$, $P=0.54$).

Simuliidae contributed the greatest biomass to the high severity burn category, though the overall effect of burn type on biomass of larval Simuliidae was marginally significant ($F_{2,9}= 3.43$, $P=0.078$). A marginally significant greater total biomass of larval Simuliidae was measured in high severity vs. unburned categories (Fig 2.4B; Dunnett, $P=0.086$) and high vs. low severity categories (Fig 2.4B; Tukey HSD, $P=0.078$) but there was no difference between unburned and low severity categories (Fig 2.4B; Dunnett, $P=0.953$). For larval Simuliidae there also was an overall (though marginally significant) effect of burn type on number of individuals ($F_{2,9} = 3.72$, $P=0.066$), with the greatest difference occurring between high severity and unburned sites (39 ± 9 vs. 6 ± 2 ind., Dunnett, $P=0.047$). Likewise, burn type had a marginally significant overall effect on emergence of adult Simuliidae (Fig 2.5C; $F_{2,9} = 3.23$, $P=0.088$). Significantly greater biomass of Simuliidae emerged from high vs. low severity burn categories (Fig 2.5C; 0.46 ± 0.15 vs. 0.31 ± 0.19 mg/m^2/day, Tukey HSD, $P=0.032$). On average, a greater biomass of Simuliidae did emerge from high severity vs. unburned reaches, but this difference was not significant (Fig 2.5C; 0.46 ± 0.15 vs. 0.08 ± 0.04 mg/m^2/day, Dunnett, $P=0.475$), and there were no significant differences in their emergence between low severity and unburned categories (Fig 2.5C; 0.31 ± 0.19 vs. 0.08 ± 0.04 mg/m^2/day,

Dunnett, $P=0.391$). There was a significant effect of time on emergence of Simuliidae ($F_{5, 28} = 3.10$, $P=0.024$). Emergence peaked in the low severity category in September and was generally greater in June and July in the high severity reaches. Thus, there was a significant interaction between time and burn type for Simuliidae ($F_{10,28} = 2.76$, $P=0.017$).

I found significant differences in the combined total larval biomass of these three r-strategist primary consumers by burn type ($F_{2,9} = 21.14$, $P = 0.0004$), with the high severity burn category having significantly greater biomass than both the unburned (Fig. 2.4B; Dunnett, $P=0.004$) and low severity categories (Fig. 2.4B; Tukey HSD, $P=0.0002$). The differences by burn category in the total numbers of these three primary consumers were generally not as strong as the differences found in biomass, but still highly significant ($F_{2,9} = 10.03$, $P= 0.005$). Thus, both greater numbers and larger sizes of individuals contributed to higher production of emergence among these three primary consumers in reaches which experienced high severity fire.

Predatory Benthic Insects

Higher production of r-strategist primary consumers coincided with greater biomass of predatory benthic insects in sites that experienced high severity fire. There was a significant overall effect of burn type on total benthic biomass of all insect predators ($F_{2,9} = 9.99$, $P = 0.005$). Both high severity and unburned categories had significantly greater total biomass of predatory insects than the low severity category (Fig. 2.4A; Tukey HSD, $P=0.002$ in high vs. low severity reaches; and Dunnett, $P=0.018$ in unburned vs. low severity reaches). On average, high severity sites had greater total biomass of predatory insects than unburned sites, but this difference was not significant

(Fig. 2.4A; Dunnett, $P=0.733$). Although there was a difference in biomass, there was not a significant difference in total numbers of predators by burn category ($F_{2,9} = 2.37$, $P=0.149$). High severity sites had 25 different predatory taxa, low severity 16 predatory taxa, and unburned 21 predatory taxa. A greater biomass of 13 of the 25 predatory taxa (Tables 2.2, 2.3) was present in high severity vs. both unburned and low severity burned sites.

Rhyacophila and Tipulidae contributed the most to the high biomass of benthic predators, as well as emergence from high severity sites vs. unburned and low severity sites. Burn type had an overall significant effect on the benthic biomass of *Rhyacophila* ($F_{2,9} = 8.49$, $P=0.009$). Both high severity and unburned categories had a significantly greater biomass of larval *Rhyacophila* than low severity sites (Fig. 2.4A; high vs. low severity reaches, Tukey HSD, $P=0.004$; and unburned vs. low severity reaches, Dunnett, $P=0.015$). However, there was no difference in benthic biomass of larval *Rhyacophila* between high severity and unburned categories (Fig. 2.4A; Dunnett, $P=0.996$). Although there were significant differences in overall benthic biomass of *Rhyacophila,* there was no significant difference in total number of *Rhyacophila* larvae by burn type ($F_{2,9} = 2.04$, $P=0.186$). Burn type did not have an overall significant effect on emergence of *Rhyacophila* ($F_{2,9} = 1.34$, $P=0.309$). However, a greater (but not significant) biomass of emergence did occur from high severity vs. both unburned and low severity categories (Fig 2.5B; 2.40 ± 0.9 vs. 0.44 ± 0.15 mg/m^2/day in high severity vs. unburned reaches, Dunnett, $P=0.626$; and 2.40 ± 0.9 vs. 0.24 ± 0.08 mg/m^2/day in high vs. low severity categories, Tukey HSD, $P=0.140$). Similar to the primary consumers there was also a significant effect of time on emergence of *Rhyacophila* ($F_{5,28} = 12.39$, $P < 0.0001$), with

much greater emergence occurring from the high severity reaches between mid-June and the end of July than in later months. There was no significant interaction between time and burn type ($F_{10,28}$ = 1.79, P = 0.109). Although there was not a significant effect of burn type when multiple sample periods were analyzed using repeated measures ANOVA, there was a significant difference in total *Rhyacophila sp.* emergence by burn type ($F_{2,9}$ = 4.48, P=0.045 by ANOVA [PROC GLM]). The difference in total emergence was driven by marginally significant differences between high severity and unburned categories (33.6 ± 13.8 vs. 4.8 ± 2.7 mg/m^2/day, Tukey HSD, P=0.091) and high vs. low severity (33.6 ± 13.8 vs. 3.5 ± 1.9 mg/m^2/day, Tukey HSD, P=0.088). A significant effect of burn type on emergence of *Rhyacophila* may not have been detected in the repeated measures analysis because peaks in *Rhyacophila* emergence were obscured when multiple sample periods were pooled for the analysis.

There was no significant difference in benthic biomass of Tipulidae by burn type, although the biomass of larval Tipulidae was greatest in the high severity category (Fig. 2.4A; $F_{2,9}$ = 2.01, P=0.189). There was also no significant difference in total number of larval Tipulidae by burn type ($F_{2,9}$ = 0.84, P=0.464). The greatest flux of Tipulidae emergence consistently occurred from the high severity category, yet burn type had no overall significant effect on emergence of Tipulidae (Fig. 2.5A; $F_{2,9}$ = 0.73, P=0.507). However, there was a significant effect of time on emergence of Tipulidae ($F_{5,28}$ = 7.09, P=0.0002). Although there was no significant interaction between time and burn type for Tipulidae ($F_{10,28}$ = 1.13, P=0.375), in general the greatest emergence occurred from unburned reaches later in the sampling period, but from high severity reaches earlier in the sampling period.

Taken together, the emergence results of *Baetis*, Chironomidae, Simuliidae, Tipulidae and *Rhyacophila* suggest that greater emergence of both primary consumers and insect predators occurred from high severity vs. low severity and unburned sites. High severity sites had a greater larval biomass of some of these taxa in the benthos, while there were no differences for other taxa between high severity and unburned category benthic samples, yet differences for all taxa were consistently revealed in the flux of adult emergence.

Physical Habitat Factors

With a significant difference by burn type ($F_{2,8}$ = 4.02, P = 0.062), two times greater photosynthetically active radiation reached stream surfaces at the high severity burn vs. unburned sites and almost seven times more reached the surface of high severity burned streams than low severity burned streams (954 ± 211 vs. 458 ± 106 μmol in high severity vs. unburned reaches; Tukey HSD, P = 0.360; and 954 ± 211 vs. 143 ± 71 μmol in high severity vs. low severity burn reaches; Tukey HSD, P = 0.059; Table 1). Although there were differences in light, there were no differences in stream temperature (as annual degree days) by burn category ($F_{2,8}$ = 0.83, P = 0.471; Table 1). In general, burn severity categories did not vary significantly in the other habitat characteristics I measured (Table 1). Stream substrate embeddedness did not differ between burn severity categories ($F_{2,9}$ = 1.66, P=0.244). The low severity burn category had marginally significant lower median substrate size than both the unburned and high severity burn categories (Table 1; 10.5 ± 3.6 vs. 20.3 ± 2.7 and 18.7 ± 2.0 cm; $F_{2,9}$ = 3.38, P = 0.080) reflecting a general trend of these sites being in slightly smaller streams ($F_{2,9}$ = 2.72, P =

0.119). There was no difference in substrate embeddedness between high severity and unburned categories ($t_{2.5} = -0.73$, $P=0.492$).

DISCUSSION

The results of this study showed that streams affected by wildfire of varying severity differed in aquatic insect assemblage composition measured in terms of benthic biomass and emergence. I found that sites that experienced high severity wildfire had the greatest biomass of r-strategist, primary consumers including Chironomidae, *Baetis*, and Simuliidae, and that these fast growing taxa made up a large portion of the total emergence from high severity sites. Shifts to more r-strategist taxa in the years immediately following wildfire have been described (Mihuc et al. 1996, Minshall et al. 1997, Minshall et al. 2001), and I found that they have persisted at least 5-years post fire in this system. Likewise, the persistent differences are even more apparent when emergence data are collected over time. A benthos sample only provides a snapshot of biomass, whereas emergence provides a temporal perspective that corresponds more closely to production (Benke and Huryn 2006). Emergence data may be a more sensitive indicator of the ecological state of the insect assemblage and may also provide better insight into possible effects across multiple trophic levels.

Not only did I observe greater numbers and biomass of primary consumers in sites which experienced high severity fire, but this increased production appeared to propagate up a trophic level to drive greater larval biomass and adult emergence of insect predators such as *Rhyacophila* and Tipulidae. The response was strongest in specialist predators like *Rhyacophila* that favor sessile consumers like larval Chironomidae and

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Simuliidae, but also have been known to ambush faster moving mayflies, like *Baetis* (Thut 1969, Martin and Mackay 1982, Otto 1993). The majority of Tipulidae genera in our study sites were predaceous; however their specific feeding ecology is largely unknown. *Rhyacophila* and Tipulidae predators may feed on other taxa, but the increases I observed are likely driven by greater availability of these *r*-strategist primary consumers. For *Rhyacophila*, a difference between high severity burned reaches and unburned reaches was only detected in emergence data, not benthic data. This could be due to the fact that there was a different complement of species emerging over the sampling period in these sites, or possibly that *Rhyacophila* inhabiting sites that experienced high severity fire are multivoltine, producing more than one cohort per year. I have evidence that there are some different species of *Rhyacophila* in high severity vs. unburned sites (Table 2), however these taxa generally make up little of the total *Rhyacophila* benthic biomass. Species of *Rhyacophila* can exhibit a wide range of life histories, including univoltinism, bivoltinism, and multivoltinism, with spring to fall emergence (Ross 1956). It is possible that in sites which experienced high severity fire, species of *Rhyacophila* with semivoltine or multivoltine life histories were more abundant, or that the same species were present in both site-types, but those in high severity sites had switched to a faster producing life history with more cohorts per year. Likely, the differences in emergence result from a combination of both different species and life history variation.

In addition to fueling increased production within the stream, increased production by both primary and secondary insect consumers can also propagate out of the stream (through insect emergence) and into the riparian zone where it may affect

terrestrial insectivores (chapter 1, Baxter et al. 2005). Thus, the timing of emergence may be important in determining prey availability for both aquatic and terrestrial predators (Nakano and Murakami 2001, Baxter et al. 2005). Not only did I observe differences in aquatic insect composition with burn severity, but I found this translated to effects on emergence more strongly in some time periods than others. Although there were differences in emergence by burn type throughout the entire sampling period, this difference was greatest in the early summer when overall emergence was at its peak, and sites that experienced high severity fire were most elevated over the other categories. Sites that experienced high severity fire also had elevated levels of emergence later into the fall. This elevated emergence could be an important prey resource for riparian consumers that specialize on emerging insects. Nakano and Murakami (2001) found that reciprocal across-habitat fluxes of prey alternately subsidized both fishes and forest birds, and that these subsidies were seasonally asynchronous, with each habitat providing the other with the greatest resources when *in situ* prey were least available. Our results suggest that disturbance by wildfire may amplify this linkage in the midterm, with sites that experienced high severity fire exporting a greater biomass of adult insects to the adjacent terrestrial habitat later into the fall.

The differences in emergence by burn category that I observed appear to be largely driven by the high production rates of *r*-strategist taxa, however the mechanism promoting greater biomass and emergence of *r*-strategist taxa in reaches that experienced high severity fire is not clear. *Baetis* and Chironomidae are successful colonists because they are able to rapidly recolonize disturbed habitats and exploit a wide range of resources (Mihuc and Minshall 1995, Mihuc et al. 1996). In addition, while not mobile at

small scales, Simuliidae are known to be able to quickly colonize new habitats by drifting. In general, streams which experience wildfire are more frequently disturbed by floods and scouring in the first few years post-fire (Robinson et al. 2005). However, neither substrate size nor percent embeddedness showed evidence of greater streambed disturbance at burned vs. unburned sites 5-years post-fire. Nonetheless, in the midterm, the high density of *r*-strategists could be carryover from a pattern which arose shortly after the fire.

The results from this study suggest the aquatic insect assemblages of sites that experienced high severity fire are more productive than both unburned sites and those that burned with low severity. However, it is unclear why these sites are more productive. One possibility is that increased insect production is being fueled by greater food resources in a bottom-up effect. However, parallel studies to this one found no evidence of higher biomass of periphyton in high severity sites (see chapter 1), or inputs of terrestrial organic matter (Breanne Jackson, University of Idaho, *unpublished data*). Furthermore, I detected no differences in annual degree days by burn category, even though the most light did enter the stream at high severity burn sites. If there were no differences in the primary factors that generally drive higher insect production (food and temperature), then it is possible that the observed increase in productivity was in a large part due to the presence of greater numbers and biomass of *r*-strategist taxa. Even though these taxa are generally smaller in size, they have very large P/B ratios, translating into high production (Huryn and Wallace 2000). *Baetis* spp. have been shown to have P/B ratios of up to 97 (Benke and Jacobi 1986) while Chironomidae have been shown to have P/B ratios of up to 120 (Jackson and Fisher 1986) and the highest known production rate

is for a species of Simuliidae (8.8 g carbon m^{-2} day^{-1}) (Wootton 1988). Differences in production may also be driven by differences in diversity, species richness, or assemblage efficiency. For instance, through a stream mesocosm experiment, Cardinale et al. (2002) showed that more diverse assemblages [filter-feeding caddisfly larvae (Insecta, Trichoptera)] were more efficient and more productive than less diverse assemblages. I observed no difference in insect diversity by burn type in the streams I studied, nor any association between diversity and productivity, yet I did observe differences in production. Thus I reason that the shift in assemblage structure to more r-strategist taxa is most likely driving the greater efficiency and productivity observed in the assemblages of sites which experienced high severity wildfire.

Disturbances of varying magnitude might result in systems with different assemblage diversity; however the difference in magnitude of disturbance to the streambeds of the different burn categories is unclear. The intermediate disturbance hypothesis (Connell 1978) suggests that intermediate levels of disturbance will yield greatest assemblage diversity. According to this hypothesis I might expect the sites in our system which experienced low severity fire to have greater diversity than both the unburned sites, or sites that experienced high severity fire. I should expect this to be the case if the low severity sites were intermediately disturbed. However, the low severity sites did not differ in diversity in the mid-term period and if anything were slightly lower in species richness than both the unburned sites and sites which experienced high severity fire. Diversity could have been higher in sites which experienced low severity fire immediately following the disturbance. Yet, I do not know if the low severity sites actually experienced an intermediate degree of disturbance. From a terrestrial

perspective the low severity sites did experience an intermediate degree burn, with the riparian vegetation burned but canopy left intact. However, this may not have translated into an intermediate degree of disturbance for the physical habitat of the stream. I do expect that immediately following the fire, high severity sites likely experienced greater streambed disturbance than low severity sites, which would have opened more habitat for colonization by disturbance adapted taxa. However, this study took place in the mid-term time period and I was unable to measure the degree streambed disturbance immediately post-fire for sites which experienced low vs. high severity fire. In the midterm, I found no evidence for differences in diversity by burn category.

The results of this study show that effects of wildfire extend over time, with consequences for stream insect assemblages through the midterm period. I found that the type of fire may have important consequences for assemblage structure and productivity. My observations support that high severity fire may result in increased productivity through shifts in the insect assemblage to include taxa with fast life histories and also through particular predator-prey pathways. However, more studies are needed to determine what factors mediate the strength and nature of these responses to wildfire. Moreover, experimental studies and quantitative foodweb assessments should be conducted to determine the mechanisms behind the patterns that I have observed.

LITERATURE CITED

Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology **76**:2019-2027.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Benke, A. C., and A. D. Huryn. 2006. Secondary production of macroinvertebrates. Pages 691-710 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, San Diego.

Benke, A. C., and D. I. Jacobi. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. Journal of the North American Benthological Society **5**:107-114.

Bisson, P. A., D. R. Montgomery, and J. M. Buffington. 2006. Valley segments, stream reaches, and channel units. Pages 23-49 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology. Academic Press, San Diego.

Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature **415**:426-429.

Clements, W. H., J. H. Van Hassel, D. S. Cherry, and J. J. Cairns. 1989. Colonization, variability, and the use of substratum-filled trays for biomonitoring benthic communities. Hydrobiologia **173**:45-53.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

Davis, J. C., G. W. Minshall, C. T. Robinson, and P. Landres. 2001. Monitoring wilderness stream ecosystems. General Technical Report RMRS-GTR-70, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

Death, R. G., and M. J. Winterbourn. 1995. Diversity Patterns in Stream Benthic Invertebrate Communities: The Influence of Habitat Stability. Ecology **76**:1446-1460.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification. Environmental Management **10**:199-214.

Gauch, H. G. J. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology **45**:83-110.

Iwata, T. 2007. Linking stream habitats and spider distribution: spatial variations in trophic transfer across a forest-stream boundary. Ecological Research **22**:619-628.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a sonoran desert stream. Ecology **67**:629-638.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, California, USA.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society **19**:573-592.

Malison, R. L. 2008a. The design and use of a light-weight floating emergence trap. M.S. Thesis Chapter 3. Idaho State University, Pocatello.

Malison, R. L. 2008b. The "Fire pulse:" Wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. M.S. Thesis Chapter 1. Idaho State University, Pocatello.

Martin, I. D., and R. J. Mackay. 1982. Interpreting the diet of Rhyacophila larvae (Trichoptera) from gut analyses: an evaluation of techniques. Canadian Journal of Zoology **60**:783-789.

Mielke, P. W., Jr. and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer Series in Statistics. 344 pp.

Mihuc, T. B., and G. W. Minshall. 1995. Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. Ecology **76**:2361-2372.

Mihuc, T. B., G. W. Minshall, and C. T. Robinson. 1996. Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. Pages 83-94 *in* J. M. E. In: Greenlee, editor. Ecological Implications of Fire in Greater Yellowstone. International Association of Wildland Fire.

Minshall, G. W. 1984. Aquatic insect-substratum relationships. Pages p. 358 *in* Ecology of Aquatic Insects. Praeger Press, N.Y.

Minshall, G. W. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management **178**:155-161.

Minshall, G. W., C. T. Robinson, and D. E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences **54**:2509-2525.

Minshall, G. W., C. T. Robinson, D. E. Lawrence, D. A. Andrews, and J. T. Brock. 2001. Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbances by wildfire. International Journal of Wildland Fire **10**:201-213.

Minshall, G. W., T. V. Royer, and C. T. Robinson. 2004. Stream ecosystem responses following the Yellowstone wildfires: the first 10 years. Pages 87-97 *in* L. Wallace, editor. After the fires: the ecology of change in Yellowstone National Park. Yale University Press, New Haven, CT.

Miyake, Y., T. Hiura, N. Kuhara, and S. Nakano. 2003. Succession in a stream invertebrate community: A transition in species dominance through colonization. Ecological Research **18**:493-501.

Miyake, Y., and S. Nakano. 2002. Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. Freshwater Biology **47**:219-230.

Moser, D. C., and G. W. Minshall. 1996. Effects of localized disturbance on macroinvertebrate community structure in relation to mode of colonization and season. American Midland Naturalist **135**:92-101.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America **98**:166-170.

Otto, C. 1993. Long-term risk sensitive foraging in *Rhyacophila nubila* (Trichoptera) larvae from two streams. Oikos **68**:67-74.

Pianka, E. R. 1970. On r- and K-selection. The American Naturalist **104**:592-597.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, W. Minshall, S. R. Reice, A. L. Sheldon, B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.

Robinson, C. T., and G. W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. Journal of the North American Benthological Society **5**:237-248.

Robinson, C. T., U. Uehlinger, and G. W. Minshall. 2005. Functional characteristics of wilderness streams twenty years following wildfire. Western North American Naturalist **65**:1-10.

Ross, H. H. 1956. Evolution and Classification of the Mountain Caddisflies. University of Illinois Press, Urbana.

Statzner, B., and V. H. Resh. 1993. Multiple-site and -year analyses of stream insect emergence: a test of ecological theory. Oecologia **96**:65-79.

Stewart, W. S., and B. P. Stark. 2002. Nymphs of North American Stonefly Genera (Plecoptera), Second edition. The Caddis Press, Columbus, OH.

Thut, R. N. 1969. Feeding habits of larvae of seven Rhyacophila (Trichoptera: Rhyacophilidae) species with notes on other life- history features. Annals of the Entomological Society of America, **62**:894-898.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago.

Townsend, C. R., and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. The Journal of Animal Ecology **45**:759-772.

Townsend, C. R., and M. R. Scarsbrook. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnology and Oceanography **42**:938-949.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. The American Naturalist **115**:667-695.

Wallace, J. B., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-86 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Ward, J. W., and J. A. Stanford. 1983. The serial discontinuity concept of lotic systems. Pages 29-42 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor.

Wootton, R. S. 1988. Very high secondary production at a lake outlet. Freshwater Biology **20**:341-346.
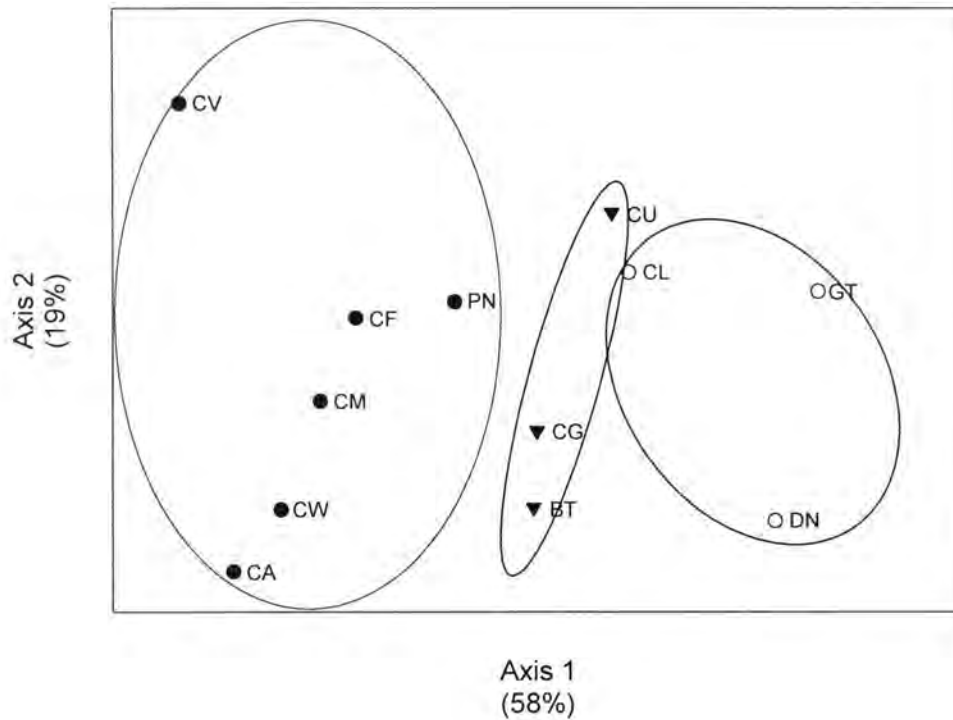
Figure 2.1. NMDS Ordination plot of 2005 benthic insect sampling sites in relative biomass ordination space. Solid circles represent sites which experience high severity fire, open circles represent sites which experienced low severity fire, and triangles represent unburned sites. Points represent a mean of 5 replicate benthic samples collected from streams (CV=Cave, CA=Calf, CW=Cow, CM=Cabin Main, CF=Cliff, PN=Pioneer, BT=Burnt, CG=Cougar, CU=Cabin Upper, CL=Cabin Lower, GT=Goat, and DN=Dunce) with different burn histories in the Big Creek Watershed. Percent of variation explained = 58% for axis 1 and 19% for axis 2. Taxa correlated (Pearson's r>0.5) with axis 1 include (from left to right): *Rhabdomastix* (-0.77), *Baetis* (-0.69), *Neophylax rickeri* (-0.65), Dytisicidae (-0.61), *Hemerodromia* (-0.58), *Rhyacophila angelitus* (-0.53), Chironomidae (-0.52), *Glutops* (0.54), Ceratopogonidae (0.58), Leuctridae (0.59), *Dixa* (0.63), *Cleptelmis* (0.67), Chloroperlidae (0.73), Leptophlebiidae (0.76), and *Oligophlebodes* (0.78). Taxa correlated with axis 2 include (from top to bottom): Chironomidae (0.69), Perlodidae (0.66), *Acentrella* (0.62), *Diphetor hageni* (0.62), *Hesperoperla* (0.62), Simuliidae (-0.57), *Zapada cinctinpes* (-0.60), and *Brachycentrus* (-0.62). The circled clusters show significant separation (by MRPP) of sites by burn severity category.
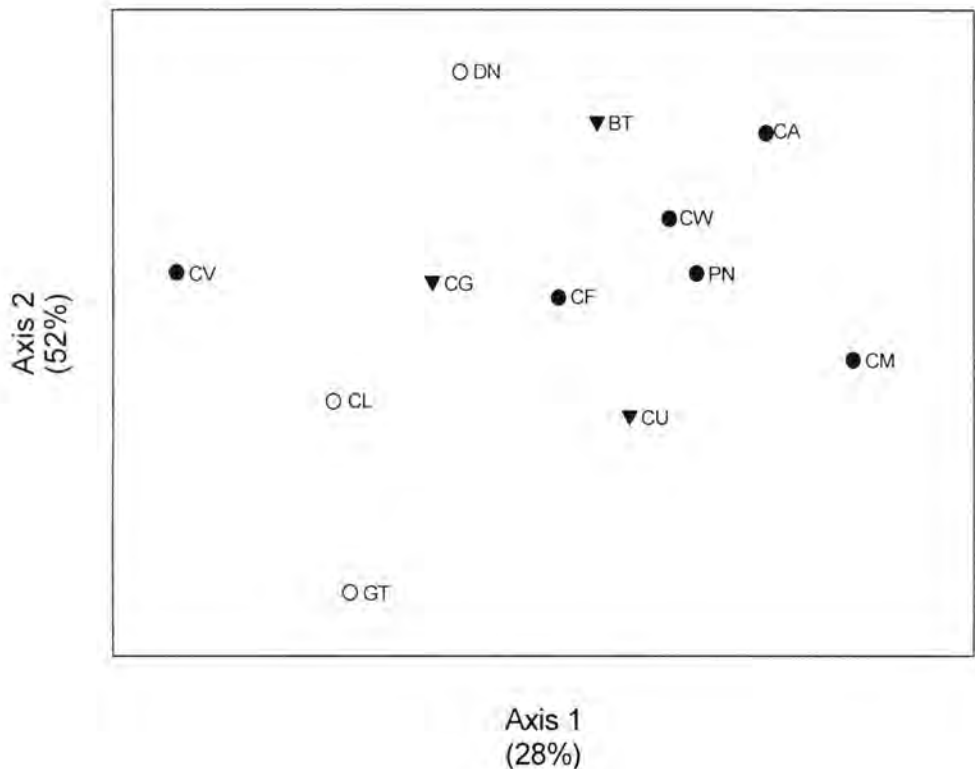
Figure 2.2. NMDS Ordination plot of 2005 emergence samples by stream in relative biomass ordination space. Solid circles represent sites which experienced high severity fire, open circles represent sites which burned with low severity fire, and triangles represent unburned sites. Points represent means of all samples collected between June and October 2005 from streams of different fire histories in the Big Creek Watershed. Percent of variation explained = 28% for axis 1 and 52% for axis 2. Taxa correlated with axis 1 include (from left to right): Chironomidae (-0.75), *Triclinocera* (-0.58), *Diphetor* (-0.57), Hydropsychidae (-0.56), Ephydridae (-0.54), *Glossosoma alascence* (0.50), *Metachela* (0.54), *Epeorus* (0.55), Rhyacophilidae (0.60), and *Rhyachophila vao* (0.76). Taxa correlated with axis 2 include (from top to bottom): Tipulidae (0.81), Simuliidae (0.54), *Paraleptophlebia* (-0.53), *Rithrogena* (-0.60), Baetidae (-0.61), and Leptophlebiidae (-0.69).
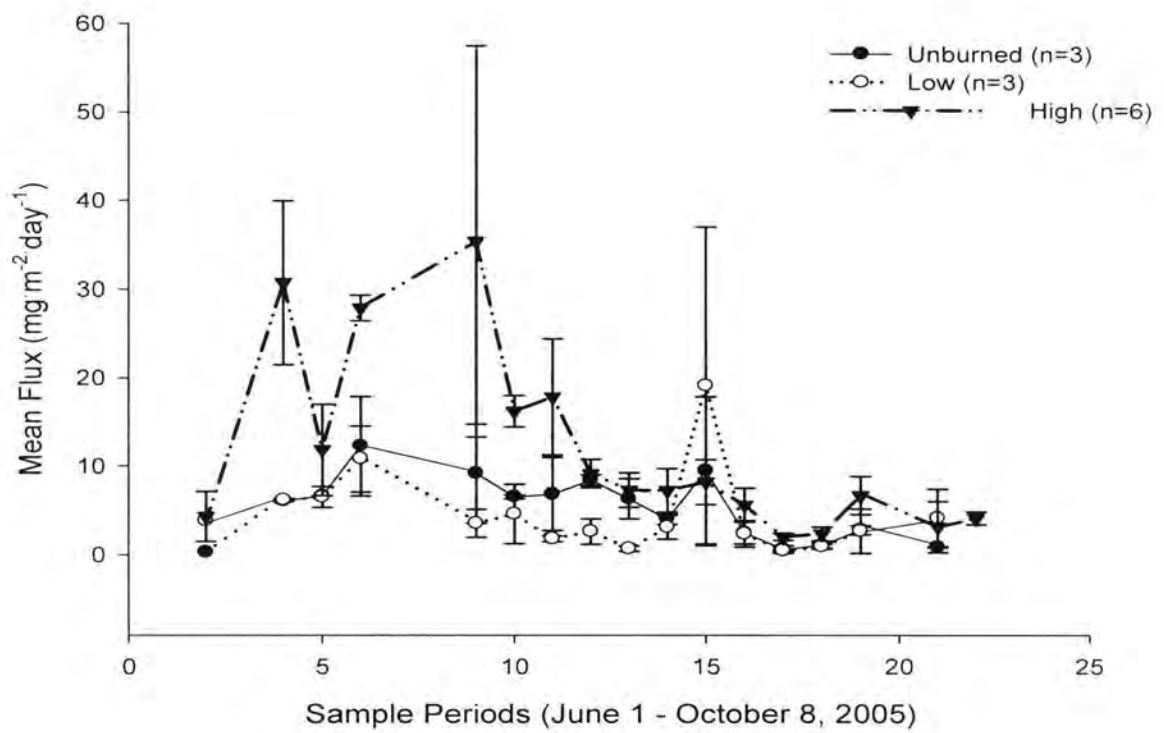
Figure 2.3. Mean flux of emergence (mean ± 1 SE) plotted by sample period for sites of different burn categories in the Big Creek Watershed for the period between June 1, 2005 and October 8, 2005.
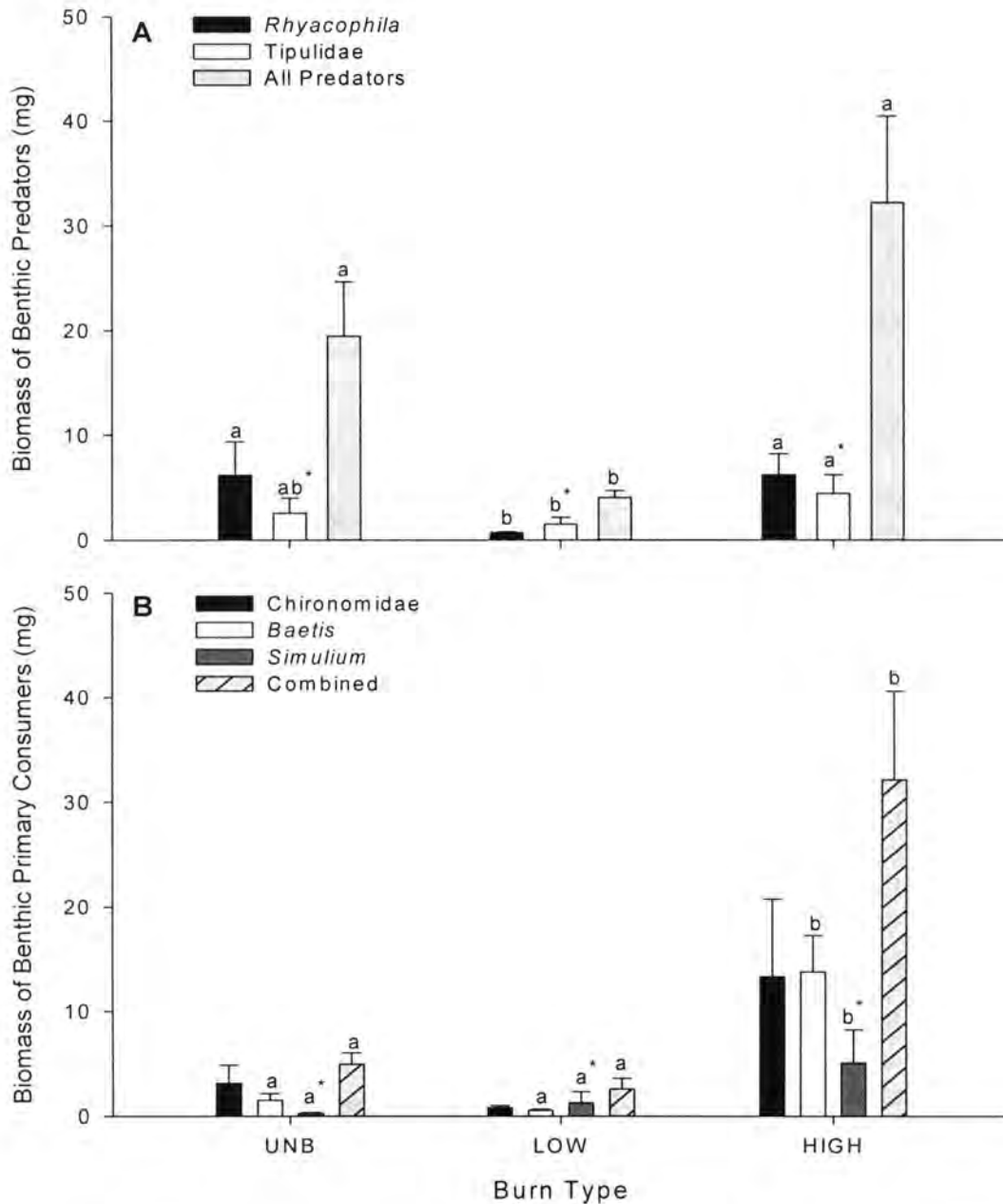
Figure 2.4. Mean total biomass (mean + 1SE) of insects in benthic samples by burn type (unburned n=3, low severity n=3, high severity n=6) collected in July 2005 from sites in the Big Creek Watershed. A) Total biomass of dominant predators in benthos samples including: Rhyacophila and Tipulidae and all predators present in benthos samples. B) Total biomass of dominant benthic primary consumers including Chironomidae, Baetis, Simuliidae and the combined prey availability of Chironomidae, Baetis, and Simuliidae biomass. Letters indicate significant differences. Letters with asterisks indicate marginally significant differences.
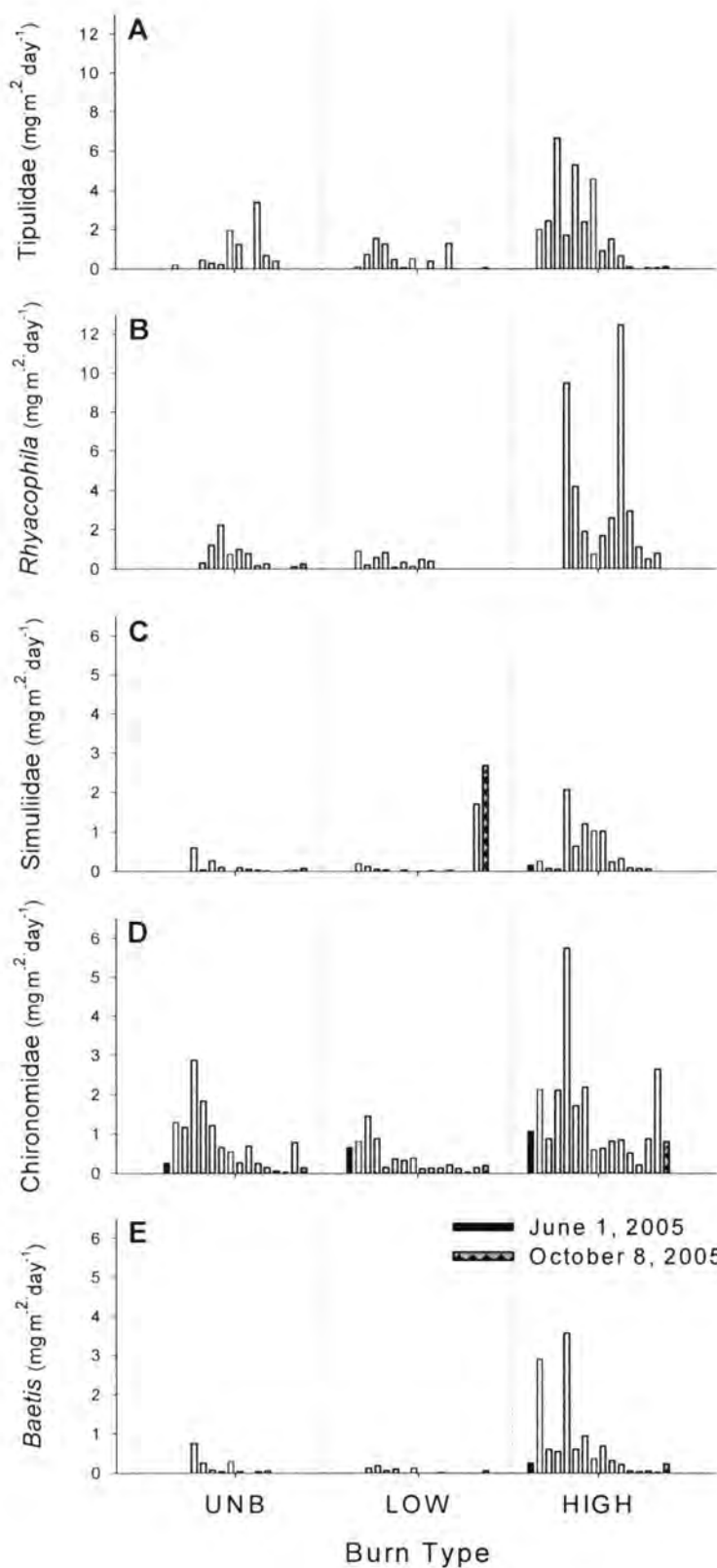
Figure 2.5. Emergence flux ($mg·m^{-2}·day^{-1}$) of three primary consumers: Chironomidae, Baetis, Simuliidae, and two predators: Tipulidae and Rhyacophila by burn type over the entire sampling period staring on June 1, 2005 and ending on October 8, 2005. Bars represent individual sample periods (average of 4 days in length), starting at the left of (the x-axis) with the beginning of the sample period on June 1, shown as a black bar (when present) and ending at the end of the sample period on October 8, shown as a checkered bar (when present). Tick marks separate different burn categories. Missing bars indicate that there was no emergence of the taxa during that sample period.

TABLES

Table 2.1. Physical habitat parameters for study sites include mean substrate size and percent embeddedness, stream aspect, elevation, annual degree days, photosynthetic active radiation (PAR), and solar insolation. Asterisks indicate data that were not collected due to logistical constraints. **Cabin Creek degree days are based on only October 20, 2005 through July 19, 2006 (10 months) due to a missing data logger. Means ± 1 standard deviation are reported, except standard errors are reported for depth.

	Site Characteristics							
	Width (m)	Depth (m)	Substrate Size (cm)	Embeddedness (% embedded)	Aspect	Elevation (m)	Annual degree days	PAR (µmol)
Unburned								
Burnt	2.82 ± 0.38	0.13 ± 0.02	24.8 ± 20.1	47 ± 39	N	1300	1993	*
Cougar	2.14 ± 0.67	0.19 ± 0.01	20.7 ± 27.9	34 ± 28	S	1180	2126	564 ± 689
NF Cabin Upper	1.18 ± 0.40	0.11 ± 0.01	15.4 ± 23.9	46 ± 23	S	1601	1649	351 ± 545
Low Severity								
Dunce	1.15 ± 0.44	0.11 ± 0.02	16.1 ± 32.3	56 ± 21	S	1165	3144	107 ± 190
Goat	0.8 ± 0.28	0.12 ± 0.01	3.9 ± 10.0	47 ± 28	S	1328	2041	42 ± 121
NF Cabin Lower	1.43 ± 0.29	0.11 ± 0.01	11.4 ± 23.8	48 ± 28	S	1584	1819	281 ± 391
High Severity								
Cabin	3.74 ± 1.16	0.24 ± 0.02	20.3 ± 17.8	50 ± 36	S	1406	955**	1417 ± 849
Calf	0.92 ± 0.29	0.09 ± 0.01	21.1 ± 33.7	47 ± 37	SW	1394	2059	99 ± 274
Cave	4.08 ± 0.99	0.21 ± 0.01	14.0 ± 16.9	37 ± 35	S	1238	2271	1184 ± 743
Cliff	3.11 ± 0.86	0.24 ± 0.02	19.6 ± 16.5	22 ± 33	S	1213	2427	1463 ± 743
Cow	1.85 ± 0.41	0.16 ± 0.01	25.5 ± 24.4	46 ± 30	SW	1373	2241	679 ± 794
Pioneer	2.68 ± 0.56	0.20 ± 0.01	11.8 ± 20.2	26 ± 28	N	1248	1937	881 ± 716

Table 2.2 Mean number and biomass for all taxa collected in benthic samples from three unburned (BT, CG, CU), three low severity burned (DN, GT, CL), and six high severity burned streams (CM, CA, CV, CW, CF, and PN). Non-insect taxa are included in this table as they were present in the stream, however, they were not included in analyses as this paper focuses only on the insect assemblage and taxa that emerge.

	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Ameletus spp.	0.6	0.022	1	0.036	2.6	0.103			1.4	0.288	6.8	0.269	0.6	0.379			1	0.094	1.2	0.162	2.8	0.964	0.6	0.009
Ameletus cooki			0.2	0.078																	0.2	0.194		
Ameletus similor	0.2	0.029			2.8	0.537					1.6	0.218												
Acentrella spp.																	6.6	1.038						
Baetis spp.	272	1.766	83	2.476	18	0.324	29	0.699	6.4	0.331	27	0.609	106	6.551	398	16.27	101	6.376	442	13.61	488	29.31	106	10.38
Diphetor hageni																	4.2	0.536						
Ephemerellidae *spp.*			2.2	0.026	97	0.240	0.2	0.000	44	0.544	158	0.325	31	0.241	11	0.097	1.2	0.017	51	0.391	33	0.196	6.2	0.035
Caudatella spp.									0.2	0.580			38	0.371					4.6	0.101				
Caudatella hystrix	2.6	0.019	0.6	0.012							1.4	0.008									9.2	0.107	14	0.127
Drunella spp.													0.2	0.004			14	0.357						
Drunella coloradensis	2	5.100	1	1.910	0.2	0.119					0.4	0.180	3	7.633	0.4	4.982			3.2	18.84	11	19.02	4.4	5.719
Drunella doddsi	0.4	0.062	1.8	0.051	32	0.271					19	0.142	79	7.122	3.4	0.119	6.6	0.139	5.2	0.285	12	0.421	7.2	4.174
Drunella flavilinea																	0.4	1.505			0.4	1.577		
Drunella grandis													1.8	0.050					0.4	0.004				
Drunella spinifera			0.8	5.504	20	1.108					69	4.367	5.8	0.637	0.6	0.025			4.2	0.124	0.6	0.018	1.2	1.014
Ephemerella	12	0.174			6.2	0.117					0.4	0.003												
Serratella tibialis	0.2	0.147	2.2	0.505	0.2	0.065			0.4	0.135	4.8	0.478	3	0.491	5.8	9.294	5.6	3.103	8.6	6.476	2.8	2.249	68	10.23
Timpanoga hecuba																	1.6	0.089						
Heptageniidae *spp.*	10	0.100	1.8	0.114	13	0.062			1.8	0.489	2.8	0.019	1.2	0.206	0.8	0.020	15	0.133	1	0.026	3.4	0.055	1.6	0.011
Cinygmula spp.	16	1.707	24	3.698	13	0.879			0.2	0.552	4.6	0.342	0.8	0.176					0.6	0.229	5.8	0.979	14	1.661
Cinygma									1.6	0.919														
Epeorus spp.	0.6	0.036	1.6	0.074	1	0.025					0.4	0.000	4.8	1.666					2.6	0.854	3.6	0.121	5	0.360
Epeorus deceptivus																					0.2	0.073		
Epeorus grandis	27	2.248											23	2.387					0.8	0.037	0.8	0.033	0.8	0.031
Epeorus longimanus	4.4	0.861	1	0.314									11	10.48	0.8	1.056			13	7.275	6.2	2.385	1	0.594
Rhithrogena spp.	19	0.705	1.6	0.109									0.8	0.063					0.2	0.029	2.4	0.093	0.6	0.032
Rhithrogena robusta	13	1.339	0.6	0.061																	1.4	0.122	2	0.165

	BT #	BT mg	CG #	CG mg	CU #	CU mg	DN #	DN mg	GT #	GT mg	CL #	CL mg	CM #	CM mg	CA #	CA mg	CV #	CV mg	CW #	CW mg	CF #	CF mg	PN #	PN mg
Leptophlebiidae *spp.*							11	1.030	15	0.482	1.4	0.039	0.4	0.017										
Paraleptophlebia *spp.*	0.4	0.005	3.2	0.127	0.8	0.011					1.8	0.033					0.6	0.048			2.2	0.061	0.4	0.003
Paraleptophlebia	6.4	0.127	22	0.867	41	0.988					3.8	0.096									6.8	0.184	0.8	0.028
Capniidae *spp.*	14	0.159			1.4	0.009					6.2	0.026	1.4	0.016	5.2	0.024			6.6	0.047			1.2	0.011
Chloroperlidae *spp.*	20	0.228			25	0.267	2.4	0.150	5.8	0.254	7.4	0.110	0.8	0.026	0.2	0.000	0.8	0.106	0.4	0.007	9.4	0.335	1.8	0.039
Paraperla *spp.*	0.2	0.141			8.2	0.399			1.2	0.880	2	0.150	0.2	0.054			0.4	0.088					0.8	0.373
Suwallia *spp.*					0.2	0.057							0.2	0.008										
Sweltsa *spp.*	40	5.482	25	6.168	15	1.193	0.8	0.468	0.4	0.710	3.6	0.321	1.4	0.116	0.8	0.214	7.2	0.912	1	0.426	38	3.833	18	1.404
Leuctridae *spp.*					0.6	0.008	1.2	0.185	0.6	0.218	7	0.076	1	0.029					0.2	0.015				
Paraleuctra *spp.*	2.4	0.201			10	0.278					5.6	0.096											0.6	0.033
Nemouridae *spp.*	7.2	0.035	3.4	0.026	16	0.076	13	0.138			39	0.152	3	0.010					4.6	0.048	1.2	0.012	7.4	0.044
Amphinemura *spp.*			5.4	0.246			1.2	0.227													9.4	0.694	8.6	0.319
Visoka cataractae	4.6	0.174			5.8	0.276					0.2	0.006												
Zapada *spp.*							37	0.887	1.8	0.332	12	0.095	20	0.132	124	2.090	26	0.450	50	0.592	40	0.411		
Zapada cinctipes	39	1.797	43	1.138	1.6	0.164	1.6	0.189	0.6	0.320			0.2	0.009							19	0.250	47	1.556
Yoraperla brevis	25	8.622			104	27.89	7.8	2.830	5.2	1.632	4.8	0.956	0.6	0.129	0.8	0.298			0.6	0.334			6.2	1.850
Perlidae *spp.*	0.2	0.006	4.4	0.242	21	0.682	1.0	0.098			9.4	0.289	1.2	0.075			4.2	0.252			22	1.251	16	0.626
Doroneuria *spp.*	0.6	1.118	1	3.879	2.6	1.078											1.2	11.31			1.8	11.07	1.8	13.07
Hesperoperla pacifica																	1.4	16.12						
Perlodidae *spp.*	3.8	0.101	0.6	0.018	6.6	0.166	1.4	0.116	5.6	0.223	11	0.251	4.2	0.078	0.4	0.027	18	0.987	3.8	0.146	1.2	0.048	12	0.625
Kogotus spp																	0.4	2.464						
Megarcys *spp.*	4	2.802	5.6	2.362									1	0.600	0.6	1.222	1.6	1.215	0.2	0.168	6.4	7.226	2.2	0.538
Pteronarcyidae *spp.*			5.6	0.035																				
Taeniopterygidae *spp.*	3.6	0.018	0.8	0.007							3.6	0.013	15	0.071	4.8	0.041			48	0.474	1.6	0.012	3.8	0.039
Taenionema *spp.*																					0.2	0.007		
Trichoptera					3.2	0.025					1.4	0.003												
Apataniidae *spp.*									0.2	0.300											0.6	0.013		
Apatania *spp.*													0.2	0.013										
Brachycentridae *spp.*							2.4	0.071			4.8	0.000	1.6	0.011			1.4	0.081						
Brachycentrus							0.2	0.360									11	39.25						
Brachycentrus							2.2	0.026					1	0.031	2.2	0.025			3.4	0.012				
Micrasema *spp.*	4.6	0.951	0.6	0.107	6.8	1.025					26	2.344	0.6	0.138			0.8	0.122					2.6	0.758
Brachycentrus pupae																	1.4	4.375						

	BT #	BT mg	CG #	CG mg	CU #	CU mg	DN #	DN mg	GT #	GT mg	CL #	CL mg	CM #	CM mg	CA #	CA mg	CV #	CV mg	CW #	CW mg	CF #	CF mg	PN #	PN mg
Glossosomatidae *spp.*							0.4	0.238							0.6	0.013			0.2	0.009	0.6	0.001		
Anagapetus *spp.*	18	0.282	21	0.049							0.2	0.004									1.2	0.010	0.6	0.005
Glossosoma *spp.*	1.2	0.087	2.4	0.070	0.4	0.003					0.8	0.026	5.2	0.966	1.4	0.155	5.4	0.147	1.2	0.055	0.4	0.002	0.6	0.013
Glossosoma pupae													3.2	4.206										
Goeracca							1.0	0.272																
Hydropsychidae *spp.*	48	1.065	13	0.210	1	0.038	1.8	0.104	2	0.820	0.6	0.006	9.6	0.353	3.2	0.200	27	0.835	3.2	0.324	28	0.959	1.4	0.041
Arctopsyche *spp.*																	2.4	6.464						
Arctopsyche grandis			0.2	0.021													0.8	14.69						
Hydropsyche *spp.*																								
Parapsyche *spp.*																			0.8	0.142				
Parapsyche almota							1	1.119																
Parapsyche elsis	1.4	14.47	1.4	19.47	0.2	1.589							0.6	12.42					0.4	0.096			0.2	1.194
Hydroptila *spp.*																			0.2	0.051				
Ochrotrichia *spp.*																	46	2.208						
Lepidostoma *spp.*	0.4	0.132	0.8	0.446			0.6	0.640			0.6	0.079									0.2	0.004		
Nectopsyche *spp.*					0.4	0.240																		
Limnephilidae *spp.*			0.2	0.005	0.2	0.019					1.6	0.232	0.2	0.004			1.2	0.128					0.2	0.003
Chyranda	0.8	0.039																						
Dicosmoecus *spp.*					0.2	0.589																		
Ecclisomyia *spp.*											0.4	0.197									1.6	0.620		
Psychoglypha *spp.*					0.2	12.07																		
Philopotamidae *spp.*													2	0.220										
Dolophilodes *spp.*	22	1.853			0.2	0.003							7	0.939			13	2.232	0.2	0.032			4.2	0.154
Goereilla							0.4	0.053																
Rhyacophila																	2	0.128	11	0.477	0.6	0.011		
Rhyacophila *spp.*			1.2	0.080	4.2	0.090	8.4	0.320	3	0.168			6.8	0.240	9.4	0.155					1.4	0.116	1.2	0.029
Rhyacophila angelita													0.2	0.380			1.6	2.354			0.6	1.714		
Rhyacophila betteni	1.4	0.040	9.5	2.877	0.6	0.006					0.6	0.017									2.8	0.246	9.4	0.398
Rhyacophila brunnea	3	12.21	1	0.381	1	0.185	0.6	0.404	0.2	0.362	1.8	0.381	2.8	2.521	1.6	4.305	0.4	1.344	2.6	3.629	6.6	5.919	8.8	2.568
Rhyacophila coloradensis											0.2	0.289												
Rhyacophila hyalinata	0.6	0.084	0.6	0.390									0.6	1.861							15	6.635		
Rhyacophila rotunda																			1.2	0.031	0.2	0.202		
Rhyacophila sibirica w/			0.4	0.043	0.2	0.016							0.2	0.010							6	0.368	5.4	0.693

	SITES																							
	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Rhyacophila sibirica	3	0.133	0.8	0.077	23	1.532					1.4	0.161	0.2	0.047	0.2	0.016					3	0.211	0.2	0.023
Rhyacophila vofixa					4.6	0.393																		
Rhyacophila verrula																					0.2	0.644		
Rhyacophila spp. pupae			0.4	7.227									0.2	0.552			0.2	0.776	0.2	0.421	0.8	2.283	4	17.17
Uenodiae *spp.*	5	0.290	1.6	0.018			4.6	0.023					107	0.531					3.4	0.033	1.6	0.030		
Neophylax spp.	8.8	0.272					0.4	0.011							0.2	0.000							0.4	0.019
Neophylax rickeri															0.2	0.643	0.8	5.294			0.2	2.149		
Neophylax occidentalis																							0.2	0.210
Neophylax splendens					0.6	0.298					0.2	0.013	0.4	0.878					0.2	0.803	1.6	4.222	1.4	5.696
Neothremma spp.					4.4	1.612	0.2	0.021			0.2	0.084												
Sericostriata surdickae	5.2	4.723			1.6	0.315																	0.4	0.068
Trichoptera *pupae*	2.8	0.721			0.4	2.906					0.8	0.605	3.2	5.183	0.2	1.343	0.8	1.826	0.8	1.953	0.6	1.754	1.6	8.619
Agathon spp.	0.2	0.027																						
Ceratopogonidae	2.2	0.075	2.2	0.103	11	0.324	11	0.264	2.2	0.137	9.4	0.172	1.6	0.092	1	0.054			1.8	0.185	0.4	0.024	0.2	0.008
Atrichopogon spp.			1.4	0.007											0.8	0.005			1	0.024	0.2	0.007	0.2	0.002
Forcipomyia spp.	0.6	0.005					0.2	0.009	0.6	0.980	0.4	0.002	0.2	0.006	3.8	0.070			1.6	0.032				
Chironomidae *spp.*	134	1.412	87	1.470	246	6.558	43	0.518	35	0.660	154	1.197	240	3.968	78	1.938	523	44.23	62	0.907	624	27.26	73	1.407
Chironomidae *pupae*	5.8	0.139	6.4	0.124	22	0.299	0.6	0.006			4.6	0.032	13	0.273	1.4	0.047	33	3.910	7	0.212	36	2.410	2	0.036
Deuterophlebia spp.																	0.2	0.006						
Ceratopogonid *pupae*																			0.2	0.036				
Dixa spp.	0.2	0.008					1.6	0.085	3.6	0.672	1	0.028			1.4	0.047					1	0.083	0.2	0.005
Empididae *spp.*							0.2	0.007					0.2	0.041										
Chelifera spp.	1.6	0.072	6.4	0.425	1.4	0.078	3.0	0.297	1.2	0.744	4.6	0.380	3.6	0.261	1.8	0.196			4	0.474	15	1.400	13	1.023
Clinocera spp.	0.6	0.031	1.4	0.031							0.2	0.004	13	0.906			7.2	1.254			20	3.303	1.6	0.055
Hemerodromia spp.															5.6	0.402	4.8	0.821	16	1.051	4.8	0.644		
Hemerodromia pupae													1.4	0.227	0.8	0.084	0.8	0.155	0.6	0.096				
Empididae *pupae*	0.8	0.107	1	0.146							0.2	0.021							0.4	0.070	2.6	0.506	0.8	0.121
Ephydridae *spp.*															0.8	0.070					0.2	0.035		
Muscidae *spp.*					0.2	0.028							0.2	0.028	1.2	0.168			0.2	0.015				
Glutops spp.	0.4	0.204			4.8	3.127	0.4	1.587	0.8	1.212	2.2	0.985	1.6	0.549			2	1.522					1	0.882
Phoridae *spp.*																							0.2	0.006
Psychodidae							0.2	0.002	0.2	0.368														
Psychodidae *pupae*			0.2	0.002					0.2	0.140														

	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Maruina spp.			0.2	0.017															0.2	0.010				
Maruina pupae																					0.2	0.026		
Pericoma spp.					9.8	0.089			0.4	0.000	39	0.074	1	0.006	1.2	0.027			3	0.063	0.2	0.003	0.2	0.002
Simuliidae pupae													0.2	0.018										
Simuliidae spp.							3.2	0.220					20	1.156										
Prosimulium spp.	2.2	0.902											0.2	0.005									0.8	0.262
Prosimulium pupae													0.4	0.274										
Simulium spp.	8.8	0.296	7.6	0.391	1	0.121	48	3.370	5	0.316	3	0.037	54	2.048	70	20.79	44	1.590	13	2.299	20	1.161	33	2.474
Simulium pupae			0.8	0.122	0.6	0.247	0.2	0.063					1.4	0.133	4	0.895	1.2	0.613	0.2	0.079	13	3.260	0.4	0.046
Tabanidae spp.																					0.2	0.062		
Tabanus spp.																					0.4	5.203		
Thaumaleidae spp.			1.2	0.035	0.4	0.005	0.4	0.006			0.4	0.001	0.2	0.021	0.2	0.022			1.6	0.107	0.8	0.064		
Tipulidae spp.			0.2	0.007			0.2	0.000	1.8	0.656			1	0.025	0.2	0.001			1.6	1.285				
Antocha spp.			1	0.045					0.4	0.190	0.6	0.000	7.8	0.536	0.2	1.211	0.2	0.115	1	0.037	2.4	0.533		
Dicranota spp.	0.6	0.068	2.4	0.219	0.2	0.007	1.2	0.120			0.6	0.087	0.2	0.009	3.2	0.588			1.8	0.148	0.8	0.285	0.4	0.097
Hexatoma spp.			1	1.252	0.4	0.638	0.8	0.103	2.4	0.117	0.6	1.550	0.2	0.055	0.2	0.035	0.6	2.025	1.8	0.361	1	2.113	0.2	1.826
Limnophila spp.					0.2	0.013					1.6	0.092									0.6	0.054	0.6	0.155
Limonia spp.																								
Tipula spp.			0.6	3.578	0.2	1.794			0.8	2.155	0.6	0.200			1.2	10.31			0.4	0.534	0.2	3.530		
Hesperoconopa spp.					0.6	0.021																		
Pedicia spp.							0.6	0.381																
Rhabdomastix spp. no											0.2	0.004	0.4	0.074	0.2	0.058	1.4	0.434	0.8	0.092				
Tipulidae pupae																					0.2	0.253		
Coleoptera													0.2	0.002	0.2	0.025								
Chrysomelidae spp.							0.2	0.261											0.4	0.044				
Curculionidae spp.															0.2	0.105								
Dytisidae spp.			0.4	0.020							0.2	0.002	0.6	0.006			2.4	0.060	0.3	0.025	0.6	0.015	0.2	0.004
Hydroratus																					2.2	0.051		
Elmidae spp.	15	0.113	21	0.128	99	0.536	4.0	0.203	25	0.296	44	0.207	55	0.687	1	0.068			2.6	0.088	36	0.773	66	0.469
Cleptelmis spp.			0.8	0.161			0.2	0.055	3.6	0.262	0.2	0.023									0.2	0.017		
Heterlimnius spp.	13	1.152	60	5.447	108	7.458	11	1.100	15	1.242	50	4.324	25	2.754			0.2	0.059	2	0.181	206	31.08	276	21.56
Lara spp.			4.2	6.994			3.8	5.106			3	8.105	1.2	0.157	0.2	0.162	1	1.171	0.4	0.111	1	1.264	0.6	0.276
Narpus spp.			0.6	0.531	0.2	0.026	16	6.683	0.2	0.160					0.2	0.017	1	0.234			0.4	0.034		

	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Optioservus spp.			0.2	0.015													130	15.38	0.3	0.092	2.8	0.283	0.2	0.027
Zaitzevia spp.							1	0.489																
Ptilodactylidae spp.									0.2	1.386														
Haliplidae													0.4	0.236										
Hydrophilidae spp.					0.2	0.048							0.2	0.002	0.6	0.082			0.4	0.124				
Ametor spp.																							0.2	0.026
Staphylinidae spp.	0.2	0.016	0.2	0.024	0.6	0.006	0.2	0.032	0.4	1.120									0.2	0.200			1.6	0.168
Stenus spp.	0.2	0.007																			1.2	0.132		
Lepidoptera spp.			0.4	0.060	0.2	0.002															0.4	0.067		
Simyra sp.															0.2	0.957								
Crambus spp.															0.4	*								
Cordulegaster spp.							0.2	0.273																
Anisoptera							1.4	27.33																
Collembola spp.	0.2	0.003	0.8	0.010	3	0.017			0.2	0.000	3.2	0.015	1.4	0.005	2	0.061	0.2	0.006	2.6	2.600	0.8	0.017	0.4	0.012
Amphipoda															0.2	*								
Copepoda																			0.2	0.200	0.4	0.001		
Lumbriculus spp.	0.2	0.976	0.2	2.079			8.6	40.64													0.8	5.829	1	6.153
Oligochaeta	38	2.573	91	2.080	107	3.032	61	9.302	25	5.972	103	1.484	35	0.841	6.6	0.804	194	2.696	25	25.00	23	0.664	170	14.28
Gastropoda							13	7.501	1.8	0.574	2	0.365	0.2	0.131	0.4	0.084			0.2	0.200				
Hydracarina	20	0.418	11	0.315	64	0.852	20	0.233	32	0.598	56	0.881	23	0.453	9.8	0.199	71	1.599	10	10.40	32	1.062	13	0.458
Nematoda	11	0.104	9.4	0.068	6.6	0.118	84	0.316	4.6	0.120	43	0.168	1.6	0.018	1.2	0.038	11	0.328	0.2	0.200	27	1.004	14	0.531
Ostracoda	158	3.740	258	4.319	230	6.709	6.2	0.169	863	27.69	394	10.26	6.6	0.139	6.8	0.219	7	0.093	11	11.00	113	2.271	100	1.808
Pelecypoda							15	2.731	1.4	0.445			0.2	0.079										
Sphaeriidae					0.2	0.153																		
Polycelis spp.									1	3.316			0.2	0.030			0.2	0.035			1	0.585	3	0.331

Table 2.3 All taxa collected in emergence traps from three unburned (BT, CG, CU), three low severity burned (DN, GT, CL), and six high severity burned streams (CM, CA, CV, CW, CF, PN). Means for the entire sampling period are provided for both numbers and biomass of each taxa.

	SITES																							
	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Diptera	0.13	0.004	0.05	-	0.02	-	0.07	0.008	0.02	0.006	0.08	-	0.05	-	0.05	-	0.04	0.001	0.11	0.003	-	-	0.03	-
Brachycera*	-	-	-	-	0.06	0.007	-	-	-	-	0.03	0.003	0.04	0.002	-	-	0.03	0.005	0.02	0.039	0.01	0.001	0.01	0.002
Anthomyiidae*	0.04	0.073	-	-	-	-	0.02	0.014	-	-	-	-	0.04	0.024	0.02	0.024	0.03	0.082	0.07	0.078	0.01	0.054	-	-
Asteliidae*	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Athericidae*	-	-	-	-	0.02	0.014	0.02	0.012	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aulacigastridae*	-	-	-	-	0.02	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blephrasaridae	-	-	0.06	0.136	0.02	0.008	-	-	-	-	-	-	0.08	0.393	-	-	-	-	0.02	0.163	0.03	0.110	0.21	0.534
Dioptopsis	-	-	-	-	0.02	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.028
Agathon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.088
Calliphoridae*	-	-	0.02	0.050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.07	0.409	-	-	-	-
Camillidae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-
Carnidae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.003
Ceratopogonidae	0.08	0.025	0.02	0.002	-	-	0.05	0.003	0.06	0.003	0.03	0.001	-	-	0.02	0.002	-	-	0.14	0.011	-	-	0.04	0.004
Forcipomyia	-	-	0.02	0.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chironomidae	3.33	0.181	26.8	0.831	15.2	0.751	4.65	0.170	13.7	0.340	19.5	0.481	12.3	0.340	7.61	0.309	59.4	5.260	19.6	0.624	33.6	2.920	16.1	0.466
Chloropidae*	-	-	0.02	0.000	0.06	0.003	-	-	0.02	-	-	-	0.19	0.003	0.02	0.001	0.11	0.007	0.05	0.003	0.06	0.002	0.15	0.006
Dixidae	0.42	0.098	0.20	0.054	0.02	0.007	0.10	0.021	0.42	0.065	-	-	-	-	0.39	0.114	-	-	0.32	0.098	0.19	0.052	0.16	0.049
Dixa	-	-	0.02	0.001	0.02	0.002	0.02	0.002	-	0.004	-	-	0.07	0.015	0.05	0.017	-	-	-	-	0.07	0.027	-	-
Dolichopodidae*	0.08	0.038	0.03	0.062	-	-	0.04	0.046	0.03	-	-	-	0.30	0.071	0.05	0.006	0.12	0.037	0.05	-	-	0.019	0.06	0.066
Drosophilidae*	0.04	-	-	-	-	-	-	-	0.02	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Empididae	1.04	0.248	0.44	0.106	0.46	0.100	0.15	0.062	0.02	0.003	0.03	0.007	0.57	0.199	0.90	0.164	2.14	0.731	2.16	0.381	2.00	0.703	1.37	0.350
Clinocera	-	-	0.05	0.011	-	-	-	-	-	-	-	-	0.04	0.036	-	-	-	-	-	-	-	-	-	-
Hemeodromia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.011	-	-	-	-	-	-	-	-
Hilara	-	-	0.05	0.017	0.02	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Memerodromins	-	-	-	-	-	-	-	-	-	-	0.02	0.001	-	-	-	-	-	-	-	-	-	-	-	-
Metachela	-	-	-	-	-	-	-	-	-	-	-	-	0.36	0.055	-	-	-	-	0.03	0.005	0.03	0.005	0.03	0.005
Neoplasta	0.04	0.007	0.28	0.046	-	-	0.16	0.039	0.09	0.015	0.02	0.001	0.64	0.089	0.08	0.010	0.31	0.078	0.05	0.004	0.06	0.007	0.09	0.019
Trichlinocera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.31	0.089	-	-	-	-	0.01	0.004
Ephydridae	-	-	0.05	0.007	0.02	0.004	-	-	0.11	0.007	-	-	0.07	0.022	-	-	0.60	0.110	-	-	0.07	0.020	0.06	0.019

	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
SITES	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Fannidae*	-	-	-	-	-	-	0.02	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	-	-
Lauxanidae*	-	-	-	-	-	-	-	-	-	0.013	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-
Mycetophilidae*	0.38	0.071	0.33	0.089	0.56	0.110	0.66	0.239	0.15	0.041	0.09	0.021	0.04	0.006	2.52	0.472	0.03	0.006	0.20	0.035	0.04	0.006	0.21	0.048
Muscidae*	0.08	0.102	0.02	-	-	0.003	0.03	0.094	-	-	-	-	-	-	-	-	-	-	0.05	0.002	0.03	0.029	-	-
Phoridae*	0.17	0.036	0.13	0.021	0.08	0.009	0.11	0.031	0.02	0.002	-	-	-	-	0.03	0.005	0.03	0.002	-	-	0.07	0.009	0.10	0.018
Psychodidae	0.04	0.005	0.04	0.005	0.02	0.002	0.04	0.007	-	-	0.04	0.003	-	-	0.05	-	-	-	0.25	0.026	0.06	0.007	0.01	0.002
Maruina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.005	0.02	-	-	-	-	-	-	-
Rhagionidae*	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-
Sarcophagidae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.021	0.01	-
Scathophagidae*	-	-	-	-	0.02	0.028	-	-	-	-	-	-	-	-	0.04	0.038	-	-	-	-	0.02	0.031	0.01	-	0.03	0.035
Sciaridae*	0.04	0.020	0.06	0.005	0.04	0.006	0.16	0.018	0.07	0.005	0.10	0.005	0.18	0.011	0.11	0.007	0.04	0.002	0.05	0.002	-	0.003	0.06	0.007
Simuliidae	0.21	0.074	0.29	0.058	0.17	0.046	1.84	1.168	0.05	0.013	0.02	0.013	2.35	0.477	1.17	0.323	0.28	0.068	1.07	0.322	5.09	1.215	0.53	0.188
Prosimulium	-	-	0.03	0.022	0.02	0.010	-	-	-	-	0.02	0.007	-	-	0.05	0.043	-	-	0.02	0.015	-	-	-	-
Simulium	0.04	0.005	0.03	0.010	-	-	0.02	0.004	0.03	0.006	0.02	0.014	0.32	0.035	0.41	0.100	0.08	0.027	0.16	0.051	0.13	0.039	-	-
Sphaeroceridae*	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-
Syrphidae*	-	-	-	-	0.04	0.078	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tabanidae	-	-	-	-	-	-	0.02	0.094	-	-	-	-	-	-	0.04	0.202	-	-	-	-	-	-	-	-
Thaumaela	-	-	0.02	0.002	0.02	0.007	0.02	0.008	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.002	-	-
Tachinidae*	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	0.04	-	-	-	0.02	0.054	-	-	-	-
Tipulidae	0.25	2.005	0.25	0.639	0.06	0.025	0.26	1.101	0.02	0.002	0.21	0.068	0.50	0.207	0.28	2.838	0.53	0.704	0.73	2.402	4.71	2.204	0.40	1.021
Tipulid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	0.104	-	-	-	-
Tipula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.368
Trichoceridae*	-	-	-	-	-	-	0.03	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	0.04	0.038	0.02	0.003	0.73	0.255	0.08	0.083	-	-	-	-	0.62	1.371	0.02	0.020	-	-	0.11	0.133	0.06	0.115	0.16	0.268
Brachycentridae	-	-	-	-	-	-	0.02	0.004	-	-	0.04	0.006	-	-	-	-	-	-	-	-	-	-	0.01	0.005
Brachycentrus	0.04	0.111	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.074	-	-	-	-	-	-
Micrasema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.010	-	-	-	-	-	-
Glossosomatidae	1.46	0.812	1.11	0.582	0.65	0.252	0.02	0.006	0.05	0.017	0.04	0.017	0.71	0.769	-	-	-	-	-	-	1.00	0.626	1.29	0.704
Anagapetus	1.67	0.584	0.42	0.205	0.58	0.202	-	-	-	-	0.02	0.008	-	-	-	-	-	-	-	-	0.15	0.072	0.84	0.416
Glossosoma	-	-	-	-	-	-	-	-	-	-	-	-	1.32	1.580	-	-	-	-	-	-	-	-	0.01	0.043
Hydrobiosidae	-	-	0.08	0.311	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydropsychidae	-	-	0.08	0.655	-	-	0.10	0.212	0.02	0.038	0.04	0.740	-	-	-	-	0.14	0.847	-	-	0.03	0.491	0.09	0.564
Arctopsyche	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.312	-	-	-	-

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	BT #	BT mg	CG #	CG mg	CU #	CU mg	DN #	DN mg	GT #	GT mg	CL #	CL mg	CM #	CM mg	CA #	CA mg	CV #	CV mg	CW #	CW mg	CF #	CF mg	PN #	PN mg
Hydropsyche	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	0.01	0.042
Parasyche elsis	-	-	-	-	-	-	0.04	0.077	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.213
Hydroptilidae	0.04	0.018	-	-	0.04	0.002	-	-	-	-	-	-	-	-	-	-	0.23	0.013	0.02	0.002	-	-	-	-
Lepidostomatidae	0.54	0.529	0.40	0.278	0.23	0.147	0.58	0.790	-	-	0.28	0.260	-	-	-	-	0.04	0.032	0.02	0.025	0.04	0.034	0.03	0.025
Cascadense	-	-	-	-	0.04	0.012	-	-	-	-	0.02	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Lepidostoma	-	-	0.05	0.022	0.08	0.054	0.02	0.022	-	-	0.04	0.026	-	-	-	-	-	-	-	-	-	-	-	-
L. unicolor	-	-	-	-	-	-	0.10	0.134	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limnephilidae	-	-	-	0.050	0.04	0.167	0.05	0.014	-	-	-	-	0.36	0.304	-	-	-	-	-	-	0.15	0.493	0.03	0.037
Chyranda	-	-	-	-	-	-	-	-	-	-	0.02	0.073	-	-	-	-	-	-	-	-	-	-	-	-
Ecclisomyia	-	-	0.13	0.128	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philopotamidae	-	-	-	-	0.02	0.026	0.03	0.025	-	-	0.06	0.079	-	-	-	-	-	-	-	-	-	-	0.06	0.067
Dolophilodes	-	-	-	-	-	-	-	-	-	-	0.13	0.122	-	-	-	-	-	-	-	-	-	-	-	-
Phryganeidae	-	-	-	-	0.02	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.039
Psychomyiidae	-	-	-	-	-	-	0.05	0.043	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhyacophila	0.04	0.138	0.23	0.272	0.63	0.865	0.15	0.272	0.07	0.067	0.09	0.173	0.56	1.455	0.23	0.680	0.28	0.407	0.32	1.121	0.69	2.736	1.50	3.164
R. angelita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.055	-	-
R. angolith	-	-	-	-	-	-	-	-	-	-	-	-	0.07	0.136	-	-	0.14	0.225	0.06	0.176	-	-	-	-
R. colorodensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13	0.360	-	-	0.22	0.770	-	-
R. hyalinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.108	-	-
R. narvae	-	-	-	-	0.02	0.022	0.08	0.048	0.06	0.044	0.02	0.014	-	-	-	-	-	-	-	-	-	-	-	-
R. oreia	-	-	-	-	-	-	0.11	0.037	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R. pellisa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.022	0.01	0.014	-	-
R. vao	-	-	0.02	0.046	0.02	0.043	-	-	-	-	-	-	0.29	0.884	0.09	0.267	-	-	0.23	0.677	-	-	0.21	0.548
Uenoidae	0.04	0.119	0.02	0.019	0.48	0.318	0.03	0.013	-	-	0.03	0.012	0.32	1.115	0.02	0.051	0.08	0.433	0.05	0.089	0.21	0.750	0.12	0.193
Neophylax	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.056	0.04	0.065
Neothrema	-	-	-	-	0.04	0.016	0.02	0.009	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. alicia	-	-	-	-	-	-	0.06	0.021	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oligophlobodes	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.015	-	-
O. sierra	-	-	-	-	0.02	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13	0.137	0.01	0.019
Ephemeroptera	0.04	0.013	0.03	0.027	-	-	0.07	0.044	-	-	0.03	0.015	0.12	0.069	0.02	0.031	0.31	0.070	0.16	0.089	0.25	0.278	0.13	0.154
Ameletus	-	-	-	-	0.13	0.767	-	-	0.03	0.022	0.02	0.015	-	-	0.02	0.128	-	-	-	-	-	-	-	-
Baetidae	-	-	0.02	0.005	0.04	0.007	-	-	0.02	0.004	0.03	0.007	0.05	0.038	-	-	0.03	0.007	0.02	0.013	-	0.031	-	-
Baetis	0.13	0.046	0.17	0.079	0.15	0.051	0.07	0.017	0.10	0.021	0.16	0.081	0.48	0.334	0.57	0.326	0.38	0.143	1.17	0.627	1.97	1.385	0.26	0.161

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	BT		CG		CU		DN		GT		CL		CM		CA		CV		CW		CF		PN	
	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg	#	mg
Diphetor	-	-	0.09	0.023	-	-	-	-	0.05	0.009	0.04	0.007	-	-	-	-	0.06	0.011	-	-	0.01	0.002	0.01	0.004
Ephemerellidae	0.04	0.656	0.02	0.026	0.13	0.170	0.02	0.013	0.34	0.611	0.07	0.314	0.18	0.669	0.09	0.089	0.03	0.040	0.16	0.369	0.04	0.352	0.04	0.072
Drunella	0.04	0.090	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.032
Heptageniidae	0.08	0.211	0.02	0.015	0.15	0.462	-	-	0.10	0.083	-	-	0.21	0.264	0.08	0.093	-	-	0.52	0.856	0.25	1.001	0.12	0.491
Cinymula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.011	-	-
Epeoris	0.04	0.011	-	-	-	-	-	-	-	-	-	-	0.14	0.358	0.02	0.026	-	-	0.07	-	0.03	0.117	-	-
Rithrogena	-	-	-	-	-	-	-	-	0.03	0.052	-	-	-	-	-	-	-	-	-	-	0.04	0.237	0.01	0.041
Leptophelebiidae	0.04	0.030	-	-	0.04	0.047	0.08	0.034	1.25	0.766	0.03	0.090	-	-	-	-	-	-	-	-	0.01	0.018	0.03	0.020
Paraleptophlebia	-	-	-	-	-	-	0.10	0.046	0.19	0.085	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	0.03	0.021	-	-	-	-	-	-
Capniidae	-	-	0.02	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.004	0.03	0.004	-	-
Chloroperlidae	-	-	0.02	0.015	0.02	-	-	-	0.06	0.100	-	-	-	-	-	-	-	-	-	-	0.06	0.100	0.06	0.081
Perlidae	0.08	3.148	0.03	0.582	-	-	-	-	0.02	0.050	-	-	-	-	-	-	0.03	0.775	-	-	0.03	1.716	0.03	0.353
Perlodidae	-	-	0.03	0.274	-	-	-	-	0.02	0.047	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leuctridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-
Nemouridae	0.04	0.012	0.02	0.011	-	-	0.08	0.035	0.02	0.018	0.03	0.036	-	-	-	-	-	-	-	-	0.04	0.022	0.03	0.008
Peltoperlidae	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pternarcyidae	0.04	0.046	-	-	0.02	0.012	-	-	0.02	0.017	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidoptera*	0.04	-	0.02	0.322	0.04	0.019	0.02	-	-	-	0.04	0.523	0.17	-	-	-	0.04	-	-	-	0.03	0.202	0.09	-
Elateridae*	-	-	-	-	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

CHAPTER 3

DESIGN, USE, AND EVALUATION OF A LIGHT-WEIGHT, FLOATING TRAP FOR MEASURING ADULT INSECT EMERGENCE FROM STREAMS

INTRODUCTION

Emergence samples have been collected by ecologists since the early 1900's (Davies 1984), however recent developments in the field of stream ecology have created new methodological needs. Aquatic insects spend the majority of their life cycles within the aquatic environment and then emerge to disperse and reproduce. Emergence occurs both through the water column, with taxa like Diptera and Trichoptera emerging directly from the water surface, while other taxa like Plecoptera and some Ephemeroptera emerge from the stream bank (Merritt et al. 2008). There is a long history of collecting emerging insects, which was primarily done by entomologists to establish taxonomy and study the biology of aquatic insects. In some cases adult aquatic insects are essential for insect identification because taxonomy based on larvae is poorly developed (Davies 1984). Many different methods have been employed to capture emerging insects, including traps placed on land (e.g. malaise traps, sticky traps), more active methods like sweep netting, or by placing traps in or on the water. Collections on land can be dominated by terrestrially derived taxa, whereas traps placed in or on the water may be more efficient when aquatic taxa are the focus of study. Historically, aquatic emergence traps were of different shapes (funnel, tent, or box shaped) and were often placed so as to enclose a patch of streambed, extending through the water column to above the water surface (see Davies 1984 for a thorough review). More recently, ecologists have begun to study

emergence of the adult phase of aquatic insects from freshwater systems as an important ecosystem flux. In this context, emergence samples can provide a cumulative measure of the production from the entire life cycles of aquatic insect taxa and can be used to estimate secondary production. The interest in sampling emergence as part of foodweb and ecosystem studies has led to new methodological needs.

The measurement of emergence as a flux in ecosystem studies was initially and briefly done within the context of constructing watershed organic matter energy budgets. These studies described emerging aquatic insects to be an insignificant portion of the overall organic matter budget (Vallentyne 1952, Fisher and Likens 1973, Meyer and Likens 1979, Webster and Patten 1979). Other early work focused on the timing and abundance of emerging adult insects (Judd 1962, Corbet 1964, Harper 1978). However, the importance of emergence has recently been acknowledged in new foodweb and flux studies, as ecologists have recognized that adult insects may play a role as a prey resource for riparian consumers, whose importance may be disproportional to the size of the flux (Nakano and Murakami 2001, Sabo and Power 2002, Iwata et al. 2003, Baxter et al. 2004, Power et al. 2004, Baxter et al. 2005). Much of the emergence that occurs from streams may not return to them, resulting in a net export of benthic production to predators in riparian zones (Jackson and Fisher 1986). For instance, Nakano and Murakami (2001) found that emergence contributed over 25% of the annual energy budget for riparian forest birds. Likewise, some guilds of web-weaving and ground-dwelling spiders, as well as beetles, bats, and lizards, derive the majority of their carbon from emerging stream insects (Power and Rainey 2000, Collier et al. 2002, Sabo and Power 2002, Paetzold et al. 2005). Because early aquatic emergence traps were often

heavy, expensive, or designed for lentic systems, ecologists have had to adapt early designs for use in foodweb and flux research. Though numerous studies have investigated the flux of adult insect emergence to terrestrial habitats (summarized in Baxter et al. 2005), a range of techniques have been applied for sampling and measuring emergence, and these methods have not been formally described or evaluated.

With the interest in measuring emergence as part of ecosystem and foodweb research has developed a need for large numbers of measurements to be made simultaneously and throughout a wide range of habitats, including remote locations. Additionally, emergence may only be a single component of an ecosystem study, and therefore the equipment needed should not constitute a large proportion of the project cost. Unfortunately, for the ecosystem ecologist, a standardized, cost-efficient method for measuring adult aquatic emergence in back-country, or other logistically difficult settings has been lacking. Here I describe the design and use of an emergence trap that is inexpensive, lightweight, and well-suited for simultaneous sampling of many locations, even those remote. In addition, using data from two different studies of Idaho streams, I evaluate the performance of the trap by comparing insect assemblage structure as measured via benthic and emergence samples, and by making similar comparisons of adult insects collected using emergence traps placed at mid-channel vs. stream bank locations to investigate the importance of trap placement.

MATERIALS AND PROCEDURES

Trap Design and Construction
This light-weight and inexpensive emergence trap can be dismantled into two pieces and carried by back-pack, allowing assembly on site. For the most part, I adapted

the designs used by others (Nakano and Murakami 2001, Baxter et al. 2004, Power 2004), that have not been formally described or evaluated, to make a trap that could be easily transported long distances on foot. Traps were shaped like pup-tents with a frame constructed of ¾" Schedule 20 poly-vinyl-chloride (pvc) pipe, were completed with a net made from no-see-um netting, and covered 1/3 m^2 (Fig. 3.1A). The trap base was constructed from four 27.75 cm pieces and two 58 cm pieces of pvc, to form a square (Fig. 3.2A). The two long pieces were placed on opposite sides of the square, while the other two sides were each made up of two short lengths of pvc, joined in the middle by t-joints. All sides were joined at the corners of the square using 90 degree elbow joints. PVC primer and glue were used to permanently connect all base joints. The upright portion of the trap frame was constructed of three 58 cm long lengths of pvc, connected by two 90 degree elbow joints (Fig. 2B). The ends of the upright portion slide into the t-joints in the base of the trap (Fig. 2C). The upright section may be permanently glued or remain detachable to facilitate trap removal if done by backpacking (so that the trap may fit on a backpack).

The net was constructed from no-see-um netting (mesh size: ~ 0.5 mm) (No See-Um netting 100% polyester knit, Outdoor Wilderness Fabrics, Inc., Caldwell, ID, USA). This netting was chosen for its white color, strength, durability, and mesh size. The white color was chosen because it blocked out less light and also provided the best visibility for collection of insects from the trap using an aspirator. Its small mesh size retained insects as small as midges, the smallest emerging insect that I expected to find in the trap. Because I wanted to get the best possible estimate of actual flux I chose a mesh size that would retain most taxa. Three pieces of material were used in net construction,

one rectangular and two that are modified pentagonal in shape (Fig. 3.3A,B). Each

pentagon was sewn onto the rectangle to create the shape of a pup tent, requiring only 2

seams to construct each net (Fig. 3.3A). The dimensions for the rectangle were 170 cm

in length (allowing 15 cm on each end to be left free of the triangle sides) by 70 cm in

width. The sides were modified pentagonal in shape and were each a single piece of

material (Fig. 3.3B). The base of the fabric was 64 cm in width and continued straight up

on the edges for 15 cm, before angling to form a triangle, with a total height of 80 cm

(Fig. 3.3B). The netting can be sewn together with a standard sewing machine and heavy

duty thread. The seams should be sewn ~1.5cm in from the edge of the material. When

assembling the net, the bottom 15 cm of each pentagon should not be sewn onto the

bottom 15 cm of each end of the central rectangle (Fig. 3.3A). The excess material

hanging below the tented area was wrapped around each side of the pvc base to secure

and seal the net to the pvc frame. A slit approximately 18" long was cut into one side of

the net to allow access for insect collection. Sticky-back Velcro was attached to both

sides of the slit and stapled to the netting to allow for multiple openings and closings of

the net. As an alternative, zippers may be used in place of Velcro, as long as they can be

well sealed at the top and bottom edges during the sampling period. The net was attached

to the pvc frame using Styrofoam floats, with a ¾ inch opening in the center (Fig. 3.2C).

Closed cell foam "funnoodle" flotation devices work best (diameter of foam: 2.6",

diameter of hole: 5/8"). Four floats, approximately 58 cm in length, were used. Each

float was cut down one side, enabling it to be clamped onto the pvc and hold the netting

in place. When completed, the cost of one trap at the time of this writing was

approximately $14.00 and took around 30-40 minutes to construct (once materials are gathered).

Deployment and Trap Use

The emergence trap is designed to float on the water surface. This method was chosen to facilitate continuous sampling while water levels rise or fall. Plastic zip ties can be used to secure the trap by placing them on the upstream corners of the trap. One zip tie around the 90° pvc joint can be used to anchor a loosely looped (to allow movement up and down with flow) second zip tie which is then placed over a piece of rebar that is driven into the stream bed. Two pieces of rebar on the upstream edge are sufficient for holding the trap in place. Alternatively, sandbags may be used to anchor traps to the stream bed.

While some emergence trap designs concentrate insects into a small area or collection device for removal, this design requires removing insects from the entire interior area of the trap. I chose not to include a collecting jar to keep the design simple and to facilitate repairs in the field, as well as to avoid using chemicals (which must be placed in the collecting jar) in streams where this was undesirable (e.g. wilderness, national parks). In our traps, insects typically aggregated in the upper portion of the net and along the seams of the material. However, when collecting insects care must be taken to check all areas of the trap. Another possible trap adaptation is the addition of a catch, a piece material sewn about 30 cm from the top of trap that catches insects that might fall from the upper portion of the trap (see below). I used an aspirator to remove emergent insects from the trap.

The aspirator has been a long time tool of the entomologist and many, often complex, designs are available for purchase. For wilderness settings, I found that simplifying the design of the aspirator made it a more efficient tool, as it was inexpensive and easily repairable. We constructed aspirators from 2 lengths of plastic tubing ½" in diameter. One piece of tubing was cut approximately 20 cm long and attached, using a coupler, to a second piece of tubing cut long enough to span the distance from the sampler to the furthest corner of the trap. A piece of mesh was placed on the sampling end of the coupler to prevent insects from travelling from the collecting chamber into the portion of the tubing used for suction. Aspirators were powered by sucking through the longer portion of tubing, creating a vacuum in the short tube into which the insects were pulled. Because the collecting end of the sampling chamber was left open constant suction was necessary to keep the insects in the tube until transferred to a vial with ethanol. The end of the aspirator can be held against the net wall, to hold insects within the tube, if all insects cannot be readily removed with one breath. Once collected, insects are transferred into a vial of ethanol for later processing in the lab. If a trap with a larger internal area is being sampled, or more money is available for supplies, it might be beneficial to purchase vacuum powered aspirators. However, my simple design allowed quick repairs in the field in the case of malfunction.

Sampling in Space and Time

The location of trap deployment, and thus the type of habitat sampled (i.e. riffles vs. pools), may determine the composition of emerging insects captured. Therefore, it may be important to select the habitat for deploying traps appropriate to the goals of a study. Because many insects drift some distance before emerging, samples from a trap

may collect insects derived from an unknown area, and there are few studies from which to infer how large an area this may be. It is unknown what proportion of insects emerge from directly below the trap, or recruit from the drift originating some meters upstream. Addressing this uncertainty may be important for understanding insect life history and behaviour, but may be of less concern when the focus is on estimating the overall flux of emergence as an ecosystem characteristic. Yet, habitat character may not only affect the composition of emergence, but also its magnitude. There have been few studies addressing this question, and the only one of which I are aware found that a greater biomass of insects emerged from pools than riffles (Iwata 2006). Although benthic samples are typically taken within riffle habitats, many aquatic insects from riffles may be carried downstream and concentrated in pools before emerging. Additionally, trap location must take into account the size of the trap, securability and floatability. Smaller traps will float in rougher water, but the larger the trap, the more drag will be exerted, and the more susceptible it will be to submergence. Trap size can be adapted for study location (e.g. water velocity), but once the traps become too large (~ 1m) the upstream side typically accumulates water and sinks. Accordingly, I chose to concentrate collection of emergence from pools, where I expected the greatest emergence to occur, and where a larger sized trap could maintain a good seal with the water surface without sinking.

Because emergence can be highly variable at different temporal scales the timing and frequency of collection should be considered. Seasonally in temperate streams, there is variation in the biomass of emergence, with the greatest biomass emerging in early spring (see Jackson and Fisher 1986, Baxter et al. 2005 for reviews). Emergence

continues throughout early spring and is the least abundant during winter. Life history of insects and the purposes of the research should be considered such that peak emergence is not missed. In the short-term, the number of days between collections must be determined. The shorter the collection periods, the less likely it is that undesirable events (e.g. rain) will occur that might negatively affect the samples or trap integrity. Additionally, shorter collection periods should ensure that fewer insects fall back into the water from the trap, allowing a more accurate estimation of the actual aquatic insect flux. Moreover, sampling often should ensure that at least some portion of the emergence that has just occurred will be collected, minimizing the losses due to mortality, ovipositing, or inclement weather. However, collection periods are constrained by how fast sites can be reached, especially in wilderness settings. I suggest sampling as often as logistically possible, which was every four to five days for my study. In addition to sampling often, repeated sampling should be conducted over a long enough time period to integrate the variability in emergence. If, for example, a study was conducted using few traps, deployed over only a period of days, results might be obtained that are not representative and spurious conclusions might be drawn. For instance, the peak emergence of one taxon could drive apparent patterns (e.g. differences between sites), which may not be present if more extensive sampling occurred in space and time.

Finally, the number of traps deployed should be carefully considered. The size of the sample area should be considered when determining the number of traps to be used. The larger the area that is being studied, the more traps will be needed, especially as habitat becomes more heterogeneous. Ideally a power analysis might be done to determine the sample size necessary to detect differences of a particular magnitude in

emergence in a chosen system. Studies on a number of small streams have detected patterns in emergence with sample sizes ranging from two to six emergence traps (Jackson and Fisher 1986, Baxter et al. 2005). For the purposes of this study, I chose to deploy 4 traps, so that if one was compromised during the sampling period I would still have a minimum sample size of three. However, I studied small streams (2-3rd order) and more might be necessary in a larger system.

ASSESSMENT

I evaluated the strengths and limitations of the emergence trap design described above, as well as the importance of trap placement, via use of data from two recent independent studies, one in the Frank Church Wilderness of central Idaho and one in the Big Hole and Teton Mountains in S.E. Idaho and western Wyoming. To evaluate the performance of the emergence trap and determine what component of the assemblage present within the stream was sampled by the emergence trap, I compared the assemblage structure of benthos and emergence samples collected as part of the Frank Church Wilderness study. To compare total flux of emergence, as well as emergence assemblage structure between traps floating on the water vs. traps placed at the water/stream bank interface, I used data from the Big Hole and Teton Mountains study.

Study Areas
Frank Church Wilderness

The first study was conducted in streams located within the Payette National Forest in central Idaho. Reaches were located on tributaries of Big Creek, which flows

into the Middle Fork of the Salmon River in the Frank Church 'River of No Return' Wilderness Area. The stream channel formed a step-pool morphology (Montgomery and Buffington 1997). The streams flow through steep, narrow valleys with forested slopes of primarily Douglas-Fir (*Pseudotsuga menziesii*) and/or Ponderosa Pine (*Pinus ponderosa*). Also present are extensive bare or sparsely vegetated areas and open areas of grass and sagebrush (*Artemisia*) are also common on the drier slopes. Dominant riparian vegetation includes Red Osier Dogwood (*Cornus sericea*), Rocky Mountain Maple (*Acer glabrum*) and Alder (*Alnus viridis*). The landscape generally receives about 40cm of precipitation, the majority of which occurs as snow, resulting in peak flows from late spring through mid-summer. The streams generally remain at baseflow conditions from late summer through winter.

For the comparison of benthos and emergence, data were used from 6 streams, of 2-3rd, that experienced high severity wildfire in 2000. The traps described above were used to measure emergence from May through October, 2005. Four traps were placed on pools in each stream and continuously collected emergence. Samples were collected every 4-5 days from May through August and bi-weekly sampling was done September through October. In addition to emergence, benthos samples were collected from random locations in systematically selected riffles (approximately every 25 meters) in each study reach once in July 2005. This provided the opportunity to determine what proportion of the invertebrates present in the stream was actually captured by this trap design.

Big Hole and Teton Mountains

The second study was conducted in streams in the Big Hole Mountains, ID, and the Teton Mountains, WY. The stream reaches were in tributaries of the Teton River and either within the Targhee National Forest or the Jedediah Smith Wilderness ranging in elevation from 1987 m to 2175 m. The stream channel formed a pool/riffle morphology (Montgomery and Buffington 1997). Upland vegetation is dominated by lodgepole pine *Pinus contorta*, Douglas fir *Pseudotsuga spp.*, Engelmann spruce *Picea engelmannii*, and blue spruce *Picea pungens* and can be immediately adjacent to the stream bank. Riparian vegetation is dominated by willow (*Salix spp.*) and dogwood (*Cornus spp.*). Precipitation is greatest between November and June, falling mainly as snow, and can average as high as 1.3 m annually in the highest elevations (Van Kirk and Jenkins 2005). High flows occur between May and July caused by snowmelt.

The objective of the second study was to compare channel traps (described above) with bank traps. This is important since some adult aquatic insects emerge from the water surface while others crawl out on the bank. The design of the two traps for this portion of the study was similar to that described above with two exceptions: 1) a "catch" was included in both designs and 2) bank traps were slightly altered from the original design (Fig. 1B). The catch was used to capture emerging insects that might otherwise reenter the water because of rain, wind, or mortality. Dimensions for the catch were 35x60 cm, allowing 3-4 cm between the catch and sides of the trap (for insects to fly up through). The corners of the catch were sewn to the corners of the trap approximately 30 cm from the top of the trap. The bank traps followed a similar design as the channel traps except that the netting panels were 30 cm longer. This allowed for the overhanging netting to be buried approximately 20 cm into the substrate, preventing

insect escape or potential predators from entering the trap. Before deployment of the bank traps, vegetation was removed and water poured on the ground to bring any terrestrial arthropods to the surface for subsequent removal from the trap area (Paetzold and Tockner 2005). However, vegetation removal was often unnecessary as traps were often deployed on gravel bars. Bank traps were positioned approximately 5 cm over the water edge with the rest of the trap on the bank. All traps were checked on a 4 day/10 day rotating schedule from mid June through September, 2006.

Statistical Analysis

To evaluate the performance of the emergence trap in the Frank Church Wilderness study, I compared the community composition of benthic invertebrate samples to the community composition of invertebrates collected in emergence traps. First, benthic and emergence data were compared at a coarse scale using taxa presence/absence data to investigate possible differences at the family level. This was done to determine which technique best represented the taxa present within the stream, as well as to determine which taxa were most likely missed or underrepresented by each sampling method (as these rare taxa must be excluded from the ordination techniques discussed below). Nonmetric multidimensional scaling (Kruskal and Wish 1978) was used to visually evaluate differences among techniques (benthos vs. emergence sampling) based on separation or overlap in invertebrate assemblage space. I then used Multi-response Permutation Procedures (MRPP) to test for significant differences in overall community composition by burn category (Mielke and Berry 2001). The NMDS ordination method is well suited to ecological data that is non-normal or discontinuous. Relative biomass values for taxa were used for all NMDS ordinations due to high

variation in raw biomass values. Rare taxa (less than 5 percent frequency of occurrence) were excluded from the data set (Gauch 1982) so these taxa did not skew the ordination. Only the orders Diptera, Ephemeroptera, Trichoptera, and Plecoptera were used for the comparison. Other orders (i.e. Coleoptera) and non insect taxa were not included in the analysis although they were present in the benthos samples, because the adult forms from these groups do not emerge from the stream. Taxa were grouped at the family or order level such that taxonomic resolution of the benthic and emergence data was similar. For benthos, the mean biomass (for each taxon) was computed for each stream by averaging the five replicates. For emergence, an overall mean for each taxon from each stream was computed by averaging the mean emergence (from 4 traps) of all the samples collected between May and October. To investigate differences between benthos and emergence for individual taxa, t-tests were conducted to compare the percent composition of the taxa driving the separation of benthic and emergence samples in species space.

To gauge the importance of including bank traps in the Big Hole and Teton Mountains study, I compared the total biomass of emergence occurring into bank versus emergence traps using a t-test. Total flux from channel and bank traps was compared within four individual streams over similar time frames (19 June – 31 July 2006) using paired t-tests. I also evaluated potential differences in community composition by trap placement either in the middle of the water column, or partially covering the stream bank. The same multivariate techniques used for the Frank Church Wilderness study were employed to detect patterns and test for differences in taxonomic composition of insects collected via water surface and bank traps. For this ordination taxa were grouped at the family or order level.

Comparison of Benthos vs. Emergence
<u>Presence-Absence</u>

Overall, insect composition measured via benthos and emergence sampling was very similar, with the greatest differences driven either by taxa that do not inhabit benthic riffle habitat, or taxa that do not emerge from the water column. Dipterans were well represented in the emergence traps, with a mean of 7.5 families present in the emergence traps and a mean of 8.7 families present in the benthos. Blephariceridae were only present in emergence samples, while Deuterophlebiidae and Pelechorhynchidae were only present in benthic samples. Ceratopogonidae, Chironomidae, Dixidae, Empididae, Ephydridae, Muscidae, Pyschodidae, Simuliidae, Tabanidae, Thaumaleidae and Tipulidae appeared in both benthic and emergence samples. It was noted that Simuliidae larvae did colonize the trap floats, possibly leading to elevated levels of emergence of this taxa (R. Malison, *personal observation*). Ephemeroptera were also well represented in emergence traps, with an average of 3.2 families found in emergence samples, and 4.5 families found in benthos samples. The families Baetidae, Ephemerellidae, Heptageniidae, and Leptophlebiidae were common in both benthos and emergence. Though present in the benthos of five out of six streams, individuals of the family Ameletidae were only collected in emergence samples from one stream. Trichoptera were well represented in the emergence samples with a mean of 5.3 families present in the emergence and a mean of 6.8 families present in the benthos. The family Apataniidae was only found in two benthic samples, while Brachycentridae, Glossosomatidae, Hydropsychidae, Hydroptilidae, Lepidostomatidae, Limnephilidae, Philopotamidae, Rhyacophilidae, and Uenoidae were found in both benthos and emergence. In contrast to Diptera,

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Ephemeroptera, and Trichoptera, Plecopterans were poorly represented in emergence traps, with an average of 6.3 families present in benthos samples and only 1.5 present in emergence samples; families included Capniidae, Chloroperlidae, Perlidae, Perlodidae, Leuctridae, Nemouridae, Peltoperlidae, Pternarcyidae, and Taeniopterygidae. This style of emergence trap, placed only over the water column, did not sufficiently sample Plecopterans due to their general behaviour of emerging on banks rather than through the water column. A bank trap (see below) would be required to more accurately sample this group.

Community Structure

Differences were observed in assemblage structure by sampling technique. An ordination of the stream means of all benthos and emergence samples collected in 2005, based on the relative biomasses of 36 taxa, yielded a solution that represented 83% of the total variation among samples (Fig. 3.4). Sampling techniques were significantly separated in community structure (A=0.091, P=0.002 by MRPP). Sampling techniques separated along Axis 2, which explained 37% of the variation in the assemblage structure. These differences were expected, with mostly bank emerging taxa (Plecoptera), and riffle dwelling taxa driving differences between sample types. Differences were most strongly driven by *Rhyacophila*, Blephariceridae, Dixidae, and Glossosomatidae, contributing greater proportions to emergence samples, and Perlodidae, Leuctridae, Taeniopterygidae, Nemouridae, Ceratopogonidae, Thaumaleidae, Baetidae, and Ephemerellidae, contributing greater proportions to benthic samples (Fig. 3.4; r-values ranging from -0.77 to -0.53 and from 0.55 to 0.80). Although there was separation between benthic and emergence techniques in species space (Axis 2, 37%), there was

actually greater variation within sample types (along Axis 1, 46%), than between sample techniques.

% Composition

Specific families within the orders Ephemeroptera, Plecoptera, Trichoptera, and Diptera all contributed to differences in assemblage structure by sampling technique. Baetidae, Ephemerellidae, Ceratopogonidae, Thaumaleidae, Perlodidae, Leuctridae, Taeniopterygidae, and Nemouridae were all consistently found in benthos samples. The family Baetidae made up almost twice as much of the percent composition of benthos samples on average than it did among emergence samples, though this difference was not statistically significant (8.4 ± 2.0 vs. 4.5 ± 1.1 % [mean $\pm$ 1SE]; $t = 2.31$, $P=0.117$). Ephemerellidae made up seven times more of the benthic assemblage than the emergence and this difference was significant (15.3 ± 4.4 vs. 2.5 ± 0.9 %; $t=2.57$, $P=0.035$). There was no significant difference in Ceratopogonidae or Thaumaleidae (0.2 ± 0.1 vs. 0.03 ± 0.0 %; $t=2.57$, $P=0.251$ and 0.2 ± 0.1 vs. 0.0 ± 0.0 %; $t=2.57$, $P=0.130$). Perlodidae and Nemouridae made up a significantly greater proportion of the benthos samples than those for emergence (1.5 ± 0.3 vs. 0.0 ± 0.0 %; $t=2.57$, P=0.004 and 0.7 ± 0.2 vs. 0.01 ± 0.0 %; $t=2.57$, $P=0.025$). There was a marginally significant difference by sample technique for the family Leuctridae, with a greater proportion of the benthos being composed of this taxa (0.03 ± 0.0 vs. 0.0 ± 0.0 %; $t=2.57$, $P=0.098$). Though rare, Taeniopterygidae were found in the benthos, but were not at all present in emergence samples.

Rhyacophilidae, Blephariceridae, and Dixidae were all consistently observed in emergence samples and Glossosomatidae were observed in half of the emergence samples. Rhyacophilidae made up a significantly greater proportion in the emergence

than in the benthos (20.6 ± 3.3 vs. 4.6 ± 1.0 %; $t=2.45$, $P=0.003$). In contrast, there was no difference between emergence and benthos samples for caddisflies of the Glossosomatidae family (0.7 ± 0.4 vs. 0.02 ± 0.0 %; $t=2.57$, $P=0.214$). There were marginally significant differences for the dipteran families Blephariceridae and Dixidae, with each being observed in greater proportion in the emergence than in the benthos (2.0 ± 1.0 vs. 0.0 ± 0.0 %; $t=2.57$, $P=0.095$ and 0.7 ± 0.4 vs. 0.02 ± 0.01 %; $t=2.57$, $P=0.099$). In addition, all taxa that composed at least 3% of either benthic or emergence samples for each stream are provided in Table 1.

Comparison of Channel vs. Bank Traps
Total Flux

A comparison of the total flux of emerging adult aquatic insects from channel vs. bank traps was not statistically significant in any of the streams (all $p > 0.15$). However, in the two larger streams, Teton and South Leigh, (wetted width > 6.0 m) there was a greater biomass of emerging insects from the bank traps, whereas the two smaller streams, North and South Forks of Mahogany, (wetted width < 2.5 m) had a greater biomass of emergence from channel traps.

Community Structure

Differences in insect assemblage structure were largely driven by variation among streams, rather than differences between methods. An ordination of the stream means of all channel and bank traps, based on the relative biomasses of 23 taxa, yielded a solution that represented 81% of the total variation among samples (Fig. 3.5). Sample types did not significantly differ in location in species space ($A=-0.003$, $P=0.434$ by MRPP). Sample types did separate along both Axis 1, which explained 45% of the variation in the

assemblage structure, and Axis 2 which explained 36% of the variation in the assemblage structure, but differences were largely stream dependent, rather than method dependent. Scores on Axis 1 were most strongly driven by Rhyacophilidae, Glossosomatidae, Perlodidae, Ameletidae, Ephemerellidae, Perlidae, and the orders Trichoptera and Diptera (Fig. 3.5; r-values ranging from -0.91 to -0.50 and from 0.50 to 0.72). Differences along Axis 2 were most strongly driven by Uenoidae, Chironomidae, Empididae, and Ephemeroptera in the positive direction, and Tipulidae, Nemouridae, Glossosomatidae, Hydropsychidae, and Simuliidae in the negative direction (Fig. 3.5; r-values ranging from -0.76 to -0.49 and 0.51 to 0.71). Two sites, Teton (T) and South Leigh (SL), did separate by trap type, with channel traps being associated with Trichoptera taxa in the positive direction and bank traps being associated with Plecoptera, Mayfly, and Diptera taxa in the negative direction. In addition, the North Fork Mahogany (NF) and South Fork Mahogany (SF) sites both separated more along Axis 2, with channel traps being associated with Diptera, Plecoptera, and Trichoptera taxa, and banks traps associated with Ephemeroptera, as well as different Diptera and Trichoptera taxa.

DISCUSSION

The inexpensive and light-weight floating trap design described here allows for many emergence samples to be taken simultaneously, making it possible to quantify ecological fluxes of aquatic insects in the context of ecosystem studies. There is potential for ecosystem research to incorporate this method at much broader scales than have occurred previously, due to the quick construction and low cost of this trap. Furthermore, this design allows measures to be made across a range of stream sizes, during periods of

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variable discharge, and in sampling locations that must be reached by hiking. Samples of emergence collected over many months can also provide a good index of aquatic insect secondary production. Use of this emergence trap design could serve as a basis for measurements that could be compared across systems. However, the use of traps like the one described here is not the only way to study emergence. For example, Power et. al. (2004) measured emergence using sticky traps. Using this method they were able to study the lateral dispersion of emerging insects, and availability to terrestrial consumers in different areas of the riparian zone, although this method does not measure flux directly. Ultimately, choices regarding sampling technique must be tailored to the research question of interest.

Ecologists study aquatic insects for a number of reasons, and methods used should be compared because different techniques may provide different perspectives on insect assemblage structure. The two methods discussed in this paper, benthos collection and emergence traps, provide different, but complementary, information. A benthos sample provides an almost complete collection of all taxa present within the stream, but represents a "snap shot" and does not yield a temporal perspective. If the focus of a study were on the insect diversity of a system, traditional benthos samples would certainly be necessary, as most taxa would be collected. Nonetheless, it also would be ideal to sample emergence, as this is a complementary tool that collects part of the assemblage that might otherwise be missed (taxa in faster water and pools), and furthermore, adult insects are often required for species level identification. Furthermore, because emergence samples provide a measure of flux of aquatic insects over time, they can provide a cumulative index of secondary production that reflects entire insect life cycles. Thus, if the focus of

a study were on ecosystem fluxes, emergence traps might be an essential tool. However, due to the temporal variability in emergence I argue that it is important to use benthos samples as a complementary tool to better determine what component of the assemblage has been captured in emergence, and also to better interpret the mechanisms behind observed differences in emergence.

Differences I observed in aquatic insect assemblage structure as measured via benthos vs. emergence were probably due to variation in habitat preferences or life history strategies of a few taxa. In general, emergence traps captured a relatively representative sample of taxa present in the stream. A suite of taxa exhibited differences by methodology, including *Rhyacophila*, Blephariceridae, Dixidae, and Glossosomatidae, with these taxa being more dominant in the emergence samples than the benthos. Blephariceridae and Dixidae were not typically collected in benthos samples, as they did not inhabit riffle habitat typically sampled using traditional techniques. Blephariceridae are in water that is too fast for surber sampling, whereas Dixidae occur in depositional habitats or in the eroded margins of streams. Thus emergence traps sampled taxa that were not collected in benthos samples, providing a complementary collection of aquatic insects for purposes of community characterization. However, *Rhyacophila* and Glossosomatidae do inhabit riffles sampled using a surber net, so there must be a different explanation for their comprising a greater proportion of the emergence. One likely mechanism may be differences in life history. Whereas a benthos sample might only collect one or two cohorts of a given taxa, emergence traps deployed over many months could collect additional cohorts. Thus, emergence traps may be used to better estimate aquatic insect secondary production than simply benthos samples with P/B

conversion factors applied. Differences by sampling technique observed among other taxa may be explained by missing periods of emergence if traps were not deployed, or larval life cycles that are sometimes longer than one year. Likewise, if taxa were very rare, they may have been unlikely to be captured due to the inherent variability of the emergence process. Finally, differences in Plecoptera (by sampling technique) were likely due to the fact that the channel emergence traps mainly collected taxa that emerged from the water column rather than the stream bank. Because stoneflies emerge from the stream banks and not the water column, Plecoptera made up a greater proportion of benthic samples and were underrepresented in emergence.

Our comparison of channel and bank traps found no differences in the total flux from channel vs. bank traps, but there were differences in the assemblages captured by the two different types of traps. The bank traps collected a suite of taxa that were not as common in the channel traps. However, the relative differences between bank and channel traps varied by stream. There were actually greater differences between streams, than between sample methodology for two sites, while the other two sites exhibited marked differences in methodology. Though variation by stream and site was strongest, some taxa like stoneflies and some mayflies (that emerge from the stream bank) were more commonly collected by bank traps. The importance of including bank traps in a study may depend on the question of interest. If the goal is to estimate total flux accurately, then it could be important to include flux from stream banks as well as from the channel. Furthermore, if most or many of the taxa in the assemblage emerge from the bank, then it would be very important to measure this flux. Plecoptera may be a more important component of emergence flux from larger rivers, thus I expect it would be

important to use bank traps in larger streams. However, if the traps are being used to make relative comparisons among small streams, then perhaps use of bank traps may not always be necessary. I conclude that the bank traps collected an important component of the emergence in terms of both total flux and community structure, taxa and flux that would have been missed if channel traps were used alone.

Evaluation of Trap Design and Performance

All sampling techniques, including emergence traps, are biased in some fashion. It is important to identify the limitations and constraints of different methods, to determine which is best suited to address questions of interest. I designed our emergence trap to minimize some known sources of potential bias. For example, I used white netting to limit the loss of light entering the trap area, because light availability is known to affect emergence (Morgan et al. 1963, Kimerle and Anderson 1967). Also, the alteration of water flow was minimized (by constructing the trap of light weight materials), allowing the trap to float freely on the water surface. To our knowledge the trap does not serve to repel or attract emergence, with the possible exception of increased numbers of Simuliidae due to float colonization.

Important questions to consider when sampling emergence are: "how accurate is the measure of emergence" and "what component of the actual emergence from a given stream reach is being trapped?" During the sampling period, some insects likely will fall out of the trap, with or without a catch or sample container. One of the greatest differences between our emergence trap and earlier designs is the lack of a sample container. A sample container has been included in other designs mainly to concentrate insects in a small area, facilitating removal. I chose not to use a sample container in

order to keep the design of the trap simple, easily reparable in the field, and to avoid the use of chemicals because our traps were left running for multiple days in the wilderness, with the possibility of being disturbed (i.e. rain storms). Furthermore, the presence of a container may introduce its own bias in that it may actually attract certain taxa more than others, specifically those taxa that prefer to oviposit in still water. By avoiding a sample container, insects were spread out inside the trap, but were still easily removed using an aspirator that was capable of reaching to all corners of the trap. The number of insects lost from the trap should depend on the length of time insects are left in the traps and also on weather conditions. Traps can be modified, by adding a catch, as was done for the Big Hole and Teton Mountains study, to make them more accurate (in terms of total flux) as insects that would fall back into the water without a catch will be retained by the trap. However, even with a catch, insects whose life histories involve quickly seeking out water for oviposition following emergence, might still be lost from the sample.

In addition to questions of accuracy, other taxonomic biases must also be considered. The placement of the traps can lead to taxonomic bias based upon what type of aquatic habitat is sampled. Due to the variable life histories of aquatic insect taxa, some taxa emerge from the water column (i.e. Diptera, Trichoptera and most Ephemeroptera), while other groups emerge by crawling up onto the stream bank (Plecoptera, and some Ephemeroptera) (Stewart and Stark 2002). Thus, a study using only channel traps would likely underestimate the biomass of taxa emerging from the stream bank. To sample emergence effectively, it may be important to have some prior knowledge of the insect assemblage. Knowledge of the biology and behavior of the targeted organisms allows for the adaptation of the sampling and study design.

I hope that this description of a portable emergence trap and the subsequent discussion of its general use, strengths, and limitations, will provide the background and structure for conducting future study of aquatic insect emergence. Sampling of emergence may be conducted more widely given the availability of a standardized tool that is economically feasible and portable. This type of emergence trap should be an important addition to the set of tools used by ecologists, as measuring emergence has utility in a number of different kinds of studies, including those of insect behavior and life history, as well as investigations focused on foodweb and ecosystem level questions.

LITERATURE CITED

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology **85**:2656-2663.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Collier, K. J., S. Bury, and M. Hibbs. 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshwater Biology **47**:1651-1659.

Davies, I. J. 1984. Sampling aquatic insect emergence. Pages 161-227 *in* J. A. D. a. F. H. Rigler, editor. A manual on methods for the assessment of secondary production in fresh waters. Galliard Ltd, Great Britain.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs **43**:421-439.

Gauch, H. G. J. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Iwata, T. 2006. Linking stream habitats and spider distribution: spatial variations in trophic transfer across a forest-stream boundary. Ecological Research **22**:619-628.

Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. Ecography **26**:325-337.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a sonoran desert stream. Ecology **67**:629-638.

Kimerle, R. A., and N. H. Anderson. 1967. Evaluation of aquatic insect emergence traps. Journal of Economic Entomology **60**:1255-1259.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, California, USA.

Malison, R. L. 2008b. The "Fire pulse:" Wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. M.S. Thesis Chapter 1. Idaho State University, Pocatello.

Malison, R. L. 2008c. Streams affected by wildfire of varying severity differ in aquatic insect assemblage structure and emergence. M.S. Thesis Chapter 2. Idaho State University, Pocatello.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Meyer, J. L., and G. E. Likens. 1979. Transport and Transformation of Phosphorus in a Forest Stream Ecosystem. Ecology **60**:1255-1269.

Mielke, P. W., Jr. and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer Series in Statistics. 344 pp.

Morgan, N. C., A. B. Waddell, and W. B. Hall. 1963. A comparison of the catches of emerging aquatic insects in floating box and submerged funnel traps. Journal of Animal Ecology **32**.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America **98**:166-170.

Paetzold, A., C. J. Schubert, and K. Tockner. 2005. Aquatic-terrestrial linkages along a braided river: riparian arthropods feeding on aquatic insects. Ecosystems **8**:748-759.

Paetzold, A., and K. Tockner. 2005. Riparian arthoropod predation affects biomass and abundance of aquatic insect emergence. *in*, Dubendorf.

Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291-314 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. Ecological consequences of habitat heterogeneity. Blackwell Scientific, Oxford, UK.

Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K. Marsee, and C. Anderson. 2004. River to watershed subsidies in an old-growth conifer forest. Pages 217-240 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. The University of Chicago Press, Chicago, IL, U.S.A.

Sabo, J. L., and M. E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology **83**:3023-3036.

Stewart, W. S., and B. P. Stark. 2002. Nymphs of North American Stonefly Genera (Plecoptera), Second edition. The Caddis Press, Columbus, OH.

Vallentyne, J. R. 1952. Insect Removal of Nitrogen and Phosphorus Compounds from Lakes. Ecology **33**:573-577.

Webster, J. R., and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs **49**:51-72.

Figure 3.1. (A) Light-weight emergence trap designed for use in wilderness, or other logistically difficult settings. (B) Modified emergence trap for collection of bank emerging taxa.
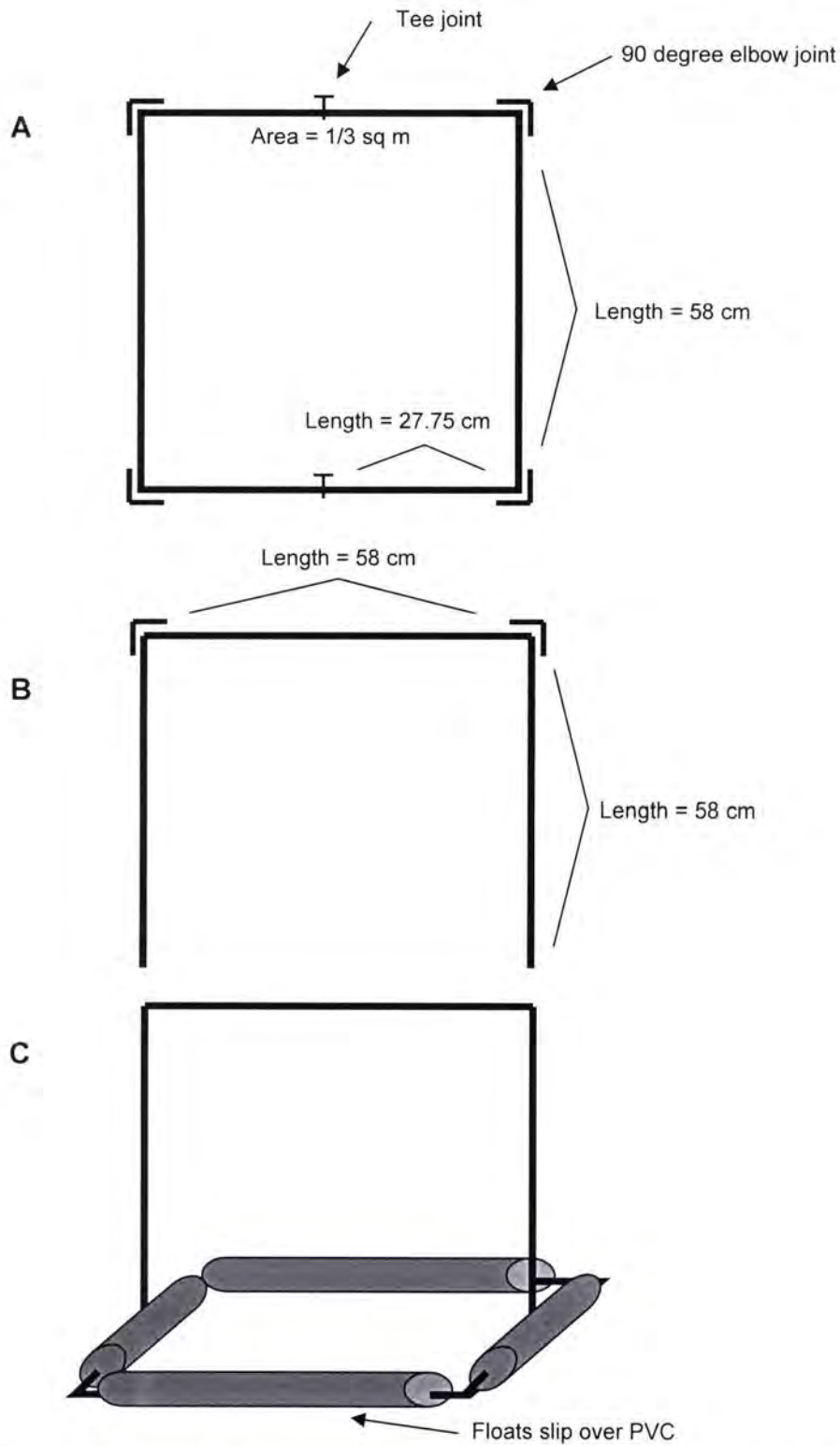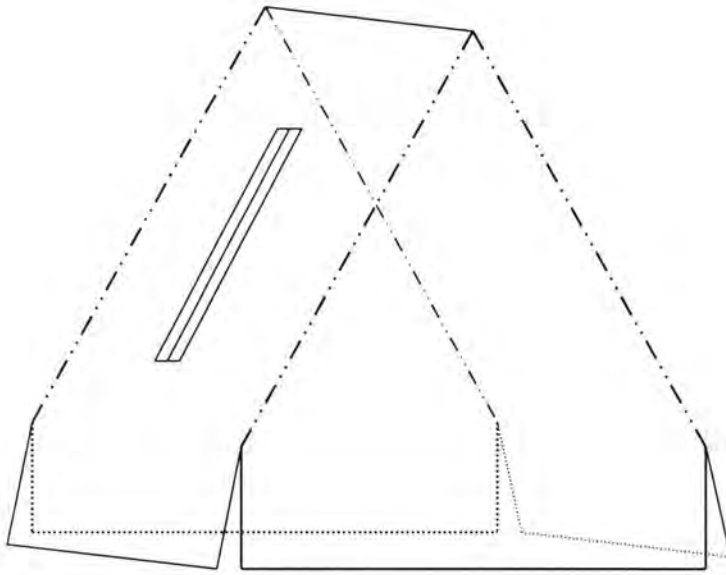
Figure 3.2. Schematic for designing the base (A) and upright section (B) of the emergence trap. (C) Floats slide over each side of the pvc frame to attach the net, as well as provide flotation.
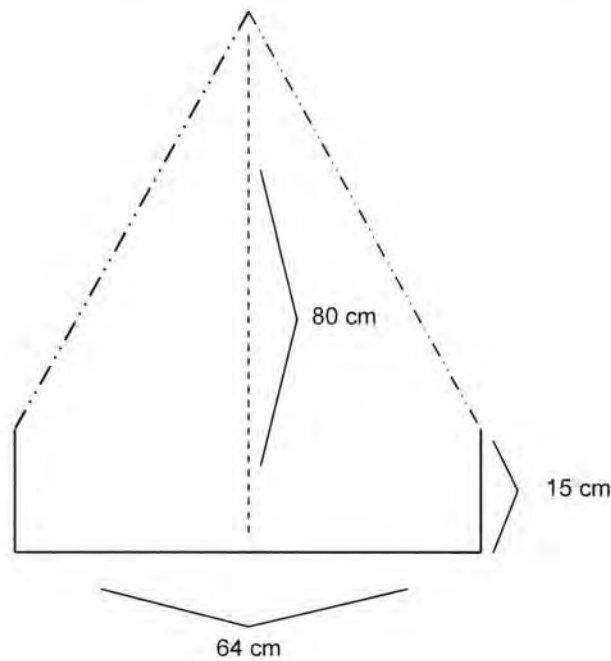
Figure 3.3. Net schematic showing dimensions for net construction. (A) Schematic showing a side piece of the net (2 needed for construction). Dashed dotted lines indicate sewing edges. The bottom rectangular area of the side piece is not attached to the rectangle piece, leaving material that can be wrapped around the pvc and attached with flotation devices. (B) Schematic of the entire net showing 2 sides connected by the long rectangle piece of material. Dashed dotted lines indicate the 2 sewing edges.
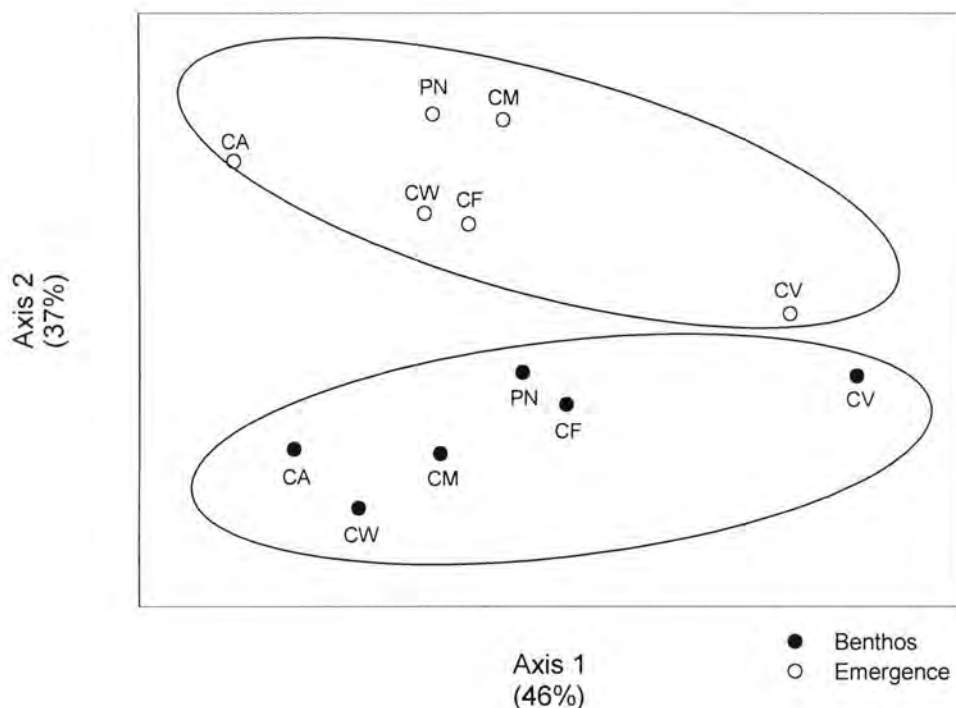
Figure 3.4. NMDS Ordination plot of 2005 benthic and emergent insect sampling sites in relative biomass taxa space. Open circles represent a mean of 5 replicate benthic samples collected once in July 2005 from streams (CA=Calf, PN=Pioneer, CM=Cabin Main, CW=Cow, CF=Cliff, CV=Cave) in the Big Creek Watershed. Filled black circles represent the mean emergence from June – October 2005. Percent of variation explained = 45.5% for axis 1 and 36.7% for axis 2. Taxa correlated with axis 1 include (from left to right): Tipulidae (-0.58), Simuliidae (-0.55), Dixidae (-0.52), Brachycentridae (0.65), Hydroptilidae (0.67), Chironomidae (0.78), and Perlidae (0.79). Taxa correlated with axis 2 include (from top to bottom): Rhyacophilidae (0.80), Blephariceridae (0.71), Dixidae (0.57), Glossosomatidae (0.55), Perlodidae (-0.53), Leuctridae (-0.54), Taeniopterygidae (-0.54), Nemouridae (-0.57), Ceratopogonidae (-0.57), Thaumaleidae (-0.61), Baetidae (-0.73), and Ephemerellidae (-0.77). The circled clusters highlight a significant difference (by MRPP) in location of benthos and emergence samples in ordination space.
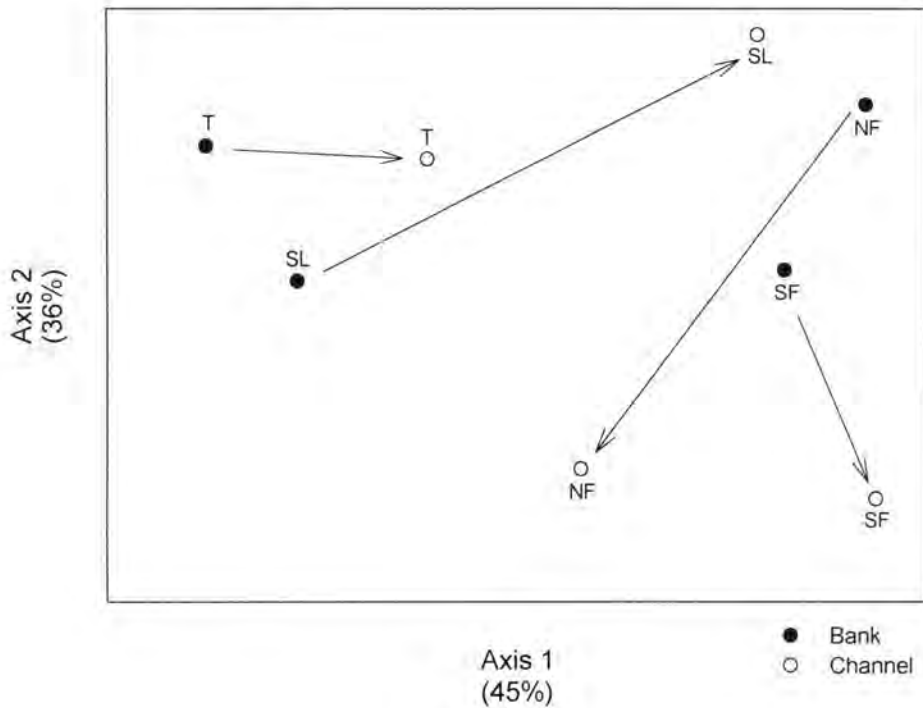
Figure 3.5. NMDS Ordination plot of mean emergence from bank and channel emergence traps in relative biomass taxa space. Open circles represent a mean of bank trap samples. Filled black circles represent the mean of channel traps. Percent of variation explained = 44.6% for Axis 1 and 36.4% for Axis 2. Taxa correlated with axis 1 include (from left to right): Perlidae (-0.91), Ephemerellidae (-0.72), Ameletidae (-0.57), Diptera (-0.54), Perlodidae (-0.50), Trichoptera (0.50), Glossosomatidae (0.59), and Rhyacophilidae (0.72). Taxa correlated with axis 2 include (from top to bottom): Uenoidae (0.71), Chironomidae (0.61), Empididae (0.57), Ephemeroptera (0.51), Tipulidae (-0.49), Nemouridae (-0.58), Glossosomatidae (-0.66), Hydropsychidae (-0.73), and Simuliidae (-0.76). The arrows show differences between bank and channel traps for individual sites in species space.

Table 1. Percent composition of taxa that made up greater than 3% of the total benthic (B) or emergence (E) biomass for streams that experienced high severity wildfire in the Big Creek Watershed. Benthic samples were collected from each stream (n=5) once in July 2005. Emergence samples were collected from June through October 2005, yielding twenty-two sampling dates, from each stream (n=4). Letters in the left most column denote orders: E=Ephemeroptera, P=Plecoptera, T=Trichoptera, and D=Diptera.

			Cabin M		Calf		Cave		Cliff		Cow		Pioneer	
			B	E	B	E	B	E	B	E	B	E	B	E
E	Baetidae	Baetis	4.7%	2.9%	12.2%	5.8%	3.1%	1.4%	9.3%	7.3%	15.7%	7.2%	4.9%	1.5%
E	Ephemerellidae										0.5%	4.2%		
E	Ephemerellidae	Drunella coloradensis	6.8%	0.0%	18.7%	0.0%			6.0%	0.0%	21.7%	0.0%	3.4%	0.0%
E	Ephemerellidae	Drunella doddsi	5.1%	0.0%										
E	Ephemerellidae	Serretella tibialis			7.0%	0.0%					7.5%	0.0%	4.9%	0.0%
E	Heptageniidae								0.0%	5.3%	0.1%	9.8%	0.0%	4.5%
E	Heptageniidae	Epeorus longimanus	12.5%	0.0%							8.4%	0.0%		
P	Perlidae	Doroneuria spp.					5.4%	0.0%	4.4%	0.0%			7.8%	0.0%
P	Perlidae	Hesperoperla pacifica					7.8%	0.0%						
P	Perlidae						0.1%	7.4%	0.4%	9.0%			0.3%	3.2%
T	Brachycentridae	Brachycentrus					18.9%	0.0%						
T	Glossosomatidae								0.0%	3.3%			0.0%	6.4%
T	Glossosomatidae	Anagapetus debilis											0.0%	3.8%
T	Glossosomatidae	Glossosoma alascense	0.0%	13.8%										
T	Hydropsychidae						0.4%	8.0%					0.0%	5.1%
T	Hydropsychidae	Arctopsyche spp.					3.1%	0.0%			0.0%	3.6%		
T	Hydropsychidae	Arctopsyche grandis					7.1%	0.0%						
T	Hydropsychidae	Parasyche elsis	22.2%	0.0%									2.8%	1.9%
T	Rhyacophilidae	Rhyacophila	0.2%	12.8%	0.1%	12.0%	0.1%	3.9%	7.7%	15.3%	0.7%	12.8%	1.8%	28.8%
T	Rhyacophilidae	Rhyacophila brunnea			4.0%	0.0%					4.2%	0.0%		
T	Rhyacophilidae	Rhyacophila coloradensis	3.3%	0.0%			0.0%	3.4%	0.0%	4.0%				
T	Rhyacophilidae	Rhyacophila hyalinata												
T	Rhyacophilidae	Rhyacophila vao	0.0%	7.7%	0.0%	4.7%					0.0%	7.8%	0.0%	5.0%
T	Uenoidae		38.0%	9.8%			0.0%	4.1%	0.0%	3.9%	4.6%	0.0%		
T	Uenoidae	Neophylax rickeri							3.4%	0.0%				