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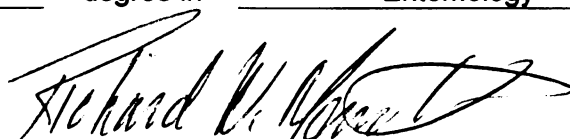
Macroinvertebrate Community Response to Timber Harvest
and Spawning Salmon in Southeast Alaska Rainforest
Streams

presented by

Emily Yvonne Campbell

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M.S. degree in Entomology



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**Macroinvertebrate Community Response to Timber Harvest and
Spawning Salmon in Southeast Alaska Rainforest Streams**

By

Emily Yvonne Campbell

A THESIS

**Submitted to
Michigan State University
In partial fulfillment of the requirements
for the degree of**

MASTER OF SCIENCE

Entomology

2010

Abstract

Macroinvertebrate Community Response to Timber Harvest and Pacific Salmon in Southeast Alaska Rainforest Streams

By

Emily Yvonne Campbell

This study examined the separate and interactive effects of timber harvest and salmon spawning on benthic macroinvertebrate community composition and distribution in Southeast Alaska streams. I predicted that 1) spawning salmon disturb benthic macroinvertebrate communities in riffles habitats and increase invertebrate drift, 2) the magnitude of spawning salmon disturbance is greater in highly harvested watersheds relative to less-impacted streams and, 3) that macroinvertebrates utilize refugia habitats such as backwater pools, stream edges, and the hyporheic zone during the salmon run to avoid riffle epilithic disturbances. Macroinvertebrates were collected quantitatively and qualitatively in multiple habitats during salmon runs on Prince of Wales Island, Alaska in 2007 and 2008. Spawning salmon caused significant declines in riffle macroinvertebrate density, biomass, and richness and the magnitude of this effect increased with increasing timber harvest intensity. In less-impacted streams, macroinvertebrate density and biomass increased. Macroinvertebrate density and richness significantly increased in stream drift during spawning. Stream edges and the hyporheic zone appear to offer refugia for macroinvertebrates during salmon spawning. This study demonstrated that timber harvest activities intensify the effects of spawning salmon disturbance on macroinvertebrate communities and that macroinvertebrates may utilize refugia in response to salmon disturbance and in Southeast Alaska streams.

To my father, for always encouraging me to pursue my academic goals and
to my mother, who's spirit will never fade.

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Chapter 1. Timber Harvest Intensifies Salmon Disturbance of Macroinvertebrate Communities in Southeast Alaskan Streams

Abstract

Natural disturbances and anthropogenic activities can interact to affect freshwater ecosystems, but these two processes are typically studied separately. We addressed how timber harvest can interact with salmon (*Oncorhynchus* spp.) spawning activities to influence benthic macroinvertebrate communities in streams on Prince of Wales Island, Alaska. We predicted that spawning salmon would cause greater disturbance to macroinvertebrates in streams from harvested watersheds, relative to less-impacted streams, because 1) finer sediments would be more readily dislodged by spawning salmon, and 2) diminished in-stream large wood would limit macroinvertebrate refugia from salmon activity. Benthic macroinvertebrates were sampled from 6 riffles within each of 7 streams before and during the annual salmon run using a modified Hess sampler. Diptera biomass was lower while Plecoptera biomass was higher during the salmon run across all streams. Macroinvertebrate density, total biomass, and the biomass of scrapers, predators, collector-gatherers and Ephemeroptera was higher during the salmon run in less-impacted streams and was lower in more harvested watersheds. Multivariate ordination demonstrated significant separation of macroinvertebrate community structure before and during the run. Indicator species analysis identified *Epeorus longimanus* (Ephemeroptera: Heptageniidae), *Baetis* (Ephemeroptera: Baetidae), *Seratella tibialis* (Ephemeroptera: Ephemerellidae), *Suwallia* (Plecoptera: Chloroperlidae), and the dipterans Chironomidae and Simuliidae as significant indicators of before-salmon benthic communities; while the stoneflies *Sweltsa* (Plecoptera:

Chloroperlidae) and *Zapada cinctipes* (Plecoptera: Nemouridae) typified during-salmon communities. Overall these results reveal that strong interactive effects can occur between anthropogenic activities and natural disturbance and show that timber-harvest activities can intensify the effects of spawning salmon disturbance on macroinvertebrates in Southeast Alaska streams.

Introduction

Human activities alter stream ecosystems worldwide and often the direct and indirect consequences of these activities are not fully understood. In Southeast Alaska, timber harvest in the form of clear-cut logging and associated road construction are major anthropogenic impacts to streams. The most common direct impact to streams is erosion and sediment deposition (Wood and Armitage 1997). Fine-sediment deposition can reduce fish populations (Jones et al. 1999, Shaw and Richardson 2001, Harvey 2009), alter macroinvertebrates (Shaw and Richardson 2001, Zweig and Rabeni 2001), algal communities (Schofield 2004), and other stream organisms including frogs (Dupuis and Stevenson 1999) and salamanders (Harvey et al. 2009). Without appropriate riparian management, logging can alter channel complexity by eliminating large wood recruitment, thereby reducing debris jams, associated downstream pools and macroinvertebrate habitats (Duncan and Brusven 1985). Over time, reductions in large wood inputs can cause a shift in channel morphology toward wider, shallower channels and finer sediment size due to fine particle erosion from unstable riparian banks (Barr and Swanston 1970, Hawkins 1982). Finer sediments can affect habitat suitability for salmon spawning and benthic communities.

Spawning salmon can have diverse effects on stream ecosystems. However, spawners affect streams via two major recognized pathways: 1) as sources of nutrients due to excretion, the release of gametes, and their decomposing carcasses, and 2) as agents of disturbance through their spawning behavior and upstream migration (Moore et al. 2004). As 'ecosystem engineers' (Jones et al. 1994, Moore and Schindler 2008) salmon have been documented to induce the massive physical disturbance and redistribution of benthic substrates during their upstream migration and redd construction (Duncan and Brusven 1985, Minakawa and Gara 2003, Tiegs et al. 2008, 2009, Monaghan and Milner 2009). In contrast to the disturbance effect, spawning salmon have been documented to provide a major resource subsidy that can positively influence stream food webs by the provision of nutrients and carbon (Gende et al. 2002, Minakawa et al. 2002, Chaloner et al. 2004, Tiegs et al. 2008). The net outcome of this enrichment and disturbance balance hinge on characteristics of the stream channel (Tiegs et al. 2008). Tiegs et al. (2008) showed that spawning salmon enrich algal communities in low-harvest watersheds with abundant wood and large sediments that likely retain salmon nutrients efficiently, and that salmon disturb algal communities in high-harvest watersheds with simplified channels and finer sediments that are more readily dislodged by spawners.

In Southeast Alaska, the legacy of logging, and healthy runs of spawning salmon, offer a unique opportunity to study the interaction between timber harvest and salmon disturbance. Others have demonstrated such an interaction for algal communities (Tiegs et al. 2008), but no studies have evaluated this effect on other components of stream food webs. I predicted that the greatest disturbance effect of macroinvertebrates due to spawning salmon would be in streams with highly harvested watersheds. I hypothesized

that: 1) spawning activity of salmon would reduce macroinvertebrate density, biomass, and taxonomic richness; 2) spawning activity would reduce disturbance-intolerant taxa and favor tolerant taxa such as predators that may feed on salmon tissues; and 3) increased timber harvest would intensify the effects of spawning salmon on macroinvertebrate community structure. This research represents the first study to assess macroinvertebrate responses to spawning salmon in relation to watershed harvest intensity.

Materials and Methods

Study sites

This study was conducted between July and September 2007 in 7 streams on Prince of Wales Island within the Tongass National Forest, Southeast Alaska, USA (Fig 1). Prince of Wales Island has a maritime climate with an annual precipitation of 0.25m and a mean air temperature of 7 °C (U.S. Department of Agriculture, Forest Service 1997). Watersheds on Prince of Wales Island are composed of coniferous temperate rainforest that has been primarily managed for timber harvest. Dominant tree species are western hemlock (*Tsuga heterophylla* (Rafinesque)), Sitka spruce (*Picea sitchensis* (Bongard)), and Western Red cedar (*Chamaecyparis nootkatensis* (D. Don)). Riparian areas that were historically harvested of timber are dominated by red alder (*Alnus rubra* (Bong)). Study streams were selected to provide a gradient of timber-harvest intensity, measured as the percentage of the watershed harvested (ranging from 5.4% to 63.8%; Table 1) but were otherwise similar in channel morphology, size, and slope. I used the

same quantifications of sediment size and large wood, and the same 300m study reaches in each stream as delineated and described by Tiegs et al. (2008).

Figure 1. Map showing the locations of the seven study streams on Prince of Wales Island, Southeast Alaska, USA.

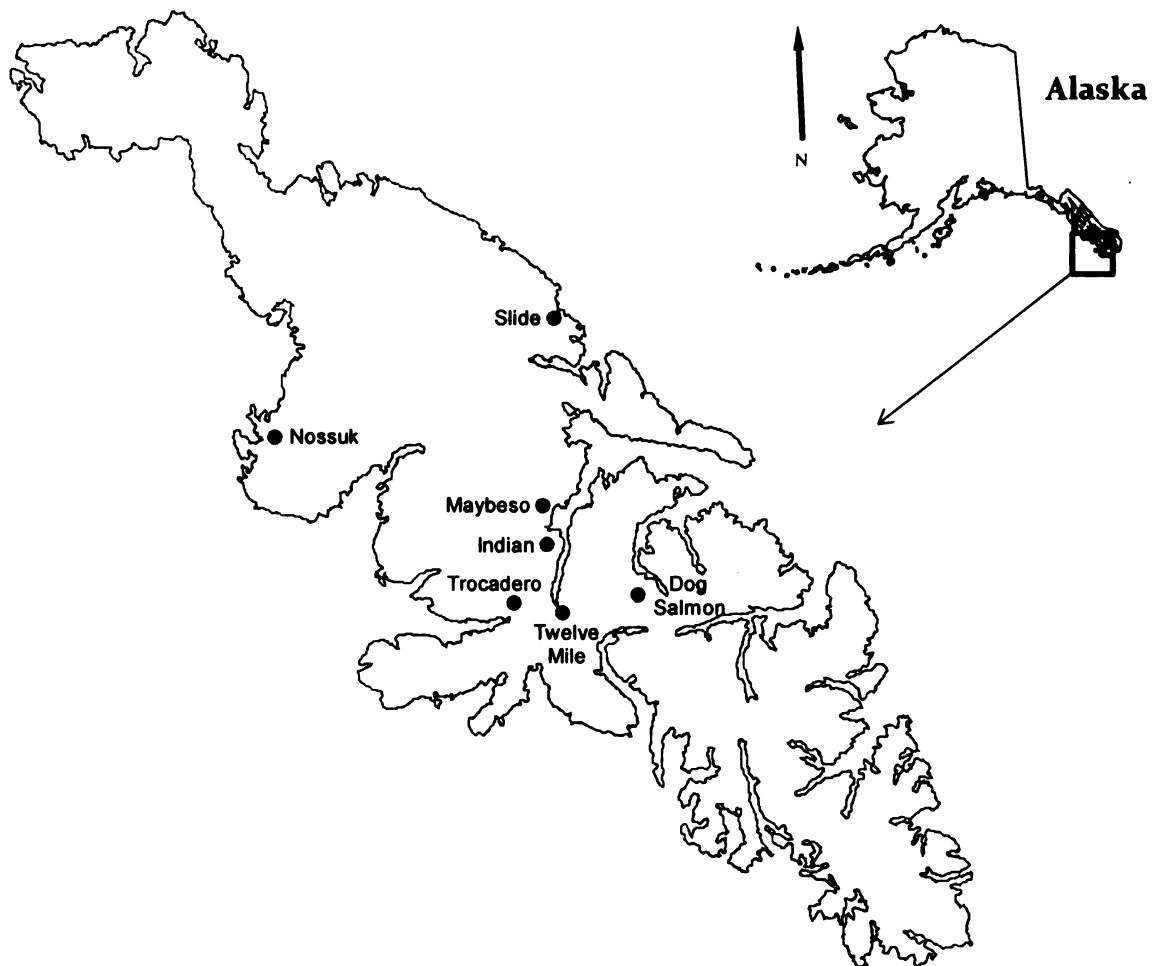


Table 1. Characteristics of the seven study streams on Prince of Wales Island, Southeast Alaska, USA. * = These values were taken from Tiegs et al. 2008. Numbers in parenthesis represent standard deviations.

Stream	*Watershed area (km ²)	*Watershed harvested (%)	*Sediment size (mm)	*Large woody debris (m ³)	Lowflow discharge (m ³ /s)	Mean daily temp. (°C)	Mean channel width (m)	Salmon density (no./m ²)
Nossuk	19.52	5.42	91.6 (81.6)	146.1	0.06	9.44 (3.05)	9.48 (1.64)	0.09
Indian	25.87	9.33	75.9 (78.4)	178.02	0.17	5.57 (4.67)	11.59 (1.47)	0.37
Trocadero	44.79	11.22	88.7 (79.3)	72.45	0.32	5.70 (4.23)	10.05 (0.27)	0.11
Dog Salmon	37.31	14.44	93.5 (67.8)	2.36	0.32	3.96 (3.40)	12.14 (1.13)	0.94
Maybeso	38.66	21.77	46.5 (32.1) 118.4	17.88	0.52	5.54 (3.77)	17.99 (1.56)	0.72
Slide	25.96	57.91	(137.6)	21.53	0.22	--	12.80 (2.14)	0.20
Twelve Mile	31.11	68.3	32.5 (37.3)	11.82	0.38	6.14 (4.18)	12.07 (0.99)	0.51

Macroinvertebrate Sampling and Processing

Benthic macroinvertebrates were quantitatively sampled in the 7 streams once before the salmon run (3-18 July) and once during the salmon run (15-20 September) from 6 riffles in each of the study streams (except Trocadero Creek that was sampled after the salmon run on 19 October). Within the 300 m delineated reach of each study stream, the first 6 riffles within the reach were sampled. A haphazardly chosen area within each riffle was selected and a single macroinvertebrate sample was collected from that area. Macroinvertebrates were collected using a modified Hess sampler with a 500- μm mesh net and a total area of 0.1 m^2 . Samples were collected by agitating the benthos by hand for 30 s to approximately 8-10 cm in depth. Samples were preserved in 70% ethanol. Macroinvertebrates were counted and identified to the lowest reliable taxon: insects were identified to genus or species (except the Chironomidae which were left at family), and non-insects were identified to class or order. Insect taxa also were measured for total length (nearest 0.5 mm) to estimate biomass based on published length-mass relationships (Benke et al. 1999). Functional feeding groups were assigned to each taxon using Merritt et al. (2008).

Salmon counts

Late-summer salmon runs were dominated by pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*). Salmon were quantified in 4 meter wide belt transects perpendicular to stream flow every 10 m for the entire 300 m reach. These counts were then up scaled to estimate the number of salmon present in the 300 m stream reach on each date. Salmon were counted from the start of the spawning run

approximately weekly for the duration of the run until mostly carcasses remained in the streams.

Statistical Analysis

I performed a repeated measures analysis of covariance (rmANCOVA) to determine whether 1) salmon presence altered macroinvertebrate abundance and taxa composition and 2) timber harvest intensity and habitat attributes (sediment size and large wood volume) influenced the level of disturbance. Macroinvertebrate response variables were density, total biomass, richness; and the biomasses of Diptera, Ephemeroptera, Plecoptera, predators, scrapers, and collector-gatherers. Sampling from before and during the salmon run was treated as the repeated factor, while, timber harvest, sediment size, and large wood were treated as covariates in separate rmANCOVAs. Although sediment size and large-wood volume are highly negatively correlated with percent timber harvest, we observed non-redundant macroinvertebrate responses to these predictor variables and thus present results of all three covariates. These analyses were conducted separately to avoid multicollinearity statistical violations. Results were considered significant when $p < 0.05$. The 6 riffles in each stream were treated as random effects, and a compound symmetric covariance structure was specified using SAS (Release 9.1; SAS Institute, Cary, North Carolina, USA).

ANCOVA assumptions were evaluated from normal probability plots, Shapiro-Wilk test statistics, and residual plots; natural logarithmic transformations were used to correct violations. Shredders, collector-filterers, and Trichoptera were rare (<0.01%, <0.02%, <0.01%, respectively, of total macroinvertebrates) and, when present, patchy in distribution and were thus omitted from analyses because they did not meet ANCOVA

assumptions. All macroinvertebrate response variables were regressed against percent timber harvest, sediment size, and large wood volume using SYSTAT (version 11; SYSTAT software, Richmond, California, USA) to establish predictive power of changes in macroinvertebrate variables due to the presence of salmon. In regression plots, the differences ('during salmon' minus 'before salmon') in macroinvertebrate response variables for each stream were used in analyses. Outlier data points in regressions were identified and removed when the Studentized residual exceeded the SYSTAT default of 2.0 or greater.

A Non-Metric Multi-Dimensional Scaling (NMDS) ordination was used to evaluate macroinvertebrate community structure differences in relation to salmon disturbance and timber harvest (McCune 2002) using PC ORD (version 5; MJM software, Gleneden Beach, Oregon, USA). I ran a total of 250 iterations for both real data and Monte Carlo analysis with a random seed start. A multiple response permutation procedure (MRPP) using Sørensen distances was performed to test for significant differences in community structure in response to salmon disturbance and among streams. When significant differences were found in macroinvertebrate community structure, Indicator Species Analysis (ISA) was used to determine which macroinvertebrate taxa were significant indicators of the respective communities. Taxa were considered significant indicators when indicator values (% of perfect indication) were >55% with $p < 0.001$. Higher indicator values demonstrate better predictive power of that taxon for its assigned group as defined by the results of the MRPP analyses. All aquatic insect taxa that represented > 3% of all samples were used in the ordination procedures.

Results

Macroinvertebrate density, biomass, and richness

Macroinvertebrate density was greater during salmon spawning in streams with low timber harvest, but was lower in streams with high timber harvest and the magnitude of this effect increased with increasing timber-harvest intensity ($R^2=0.50$, $p=0.07$; Fig. 2A, Table 2 and 5). A significantly greater disturbance effect on macroinvertebrate density was observed in streams that had finer sediments ($R^2=0.74$, $p=0.02$; Fig. 3A, Table 3) and lower volumes of large wood ($R^2=0.71$, $p=0.03$; Fig. 4A, Table 4).

Aquatic-insect biomass was significantly greater before than during the salmon run ($p=0.012$; Table 2) and a significantly greater reduction in insect biomass during the salmon run occurred in streams with high timber harvest as compared to those with low timber harvest ($R^2=0.70$, $p=0.01$; Fig. 2B, Table 2 and 5). In streams with finer sediments, salmon had a significantly greater disturbance effect on insect biomass ($R^2=0.78$, $p=0.02$; Fig. 3B, Table 3). Insect biomass also differed significantly before and during the salmon run when large wood was treated as a covariate ($p=0.014$; Table 4), with biomass being significantly higher before the salmon run. Spawning salmon had a highly significant disturbance effect on insect biomass in streams with low volumes of large wood as compared to streams with higher volumes of large wood ($R^2=0.93$, $p=0.002$; Fig. 4B, Table 4).

Macroinvertebrate taxa richness declined across all streams during the salmon run. Significantly greater macroinvertebrate richness was observed before the salmon run when timber harvest was treated as a covariate ($p=0.041$; Table 2 and 5). We found a significant salmon-sediment size interaction ($p=0.038$, Table 3) suggesting a greater disturbance effect on richness in streams that had finer sediments. A greater disturbance effect of salmon on richness was observed in streams that had low volumes of large wood as compared to streams with higher volumes of large wood ($p=0.008$, Table 4).

Figure 2. Linear regressions of the difference ('during salmon' - 'before salmon') of macroinvertebrate density (A), total insect biomass (B); and biomasses of Diptera (C), Ephemeroptera (D), gathering-collectors (E), and scrapers (F) regressed against % timber harvest.

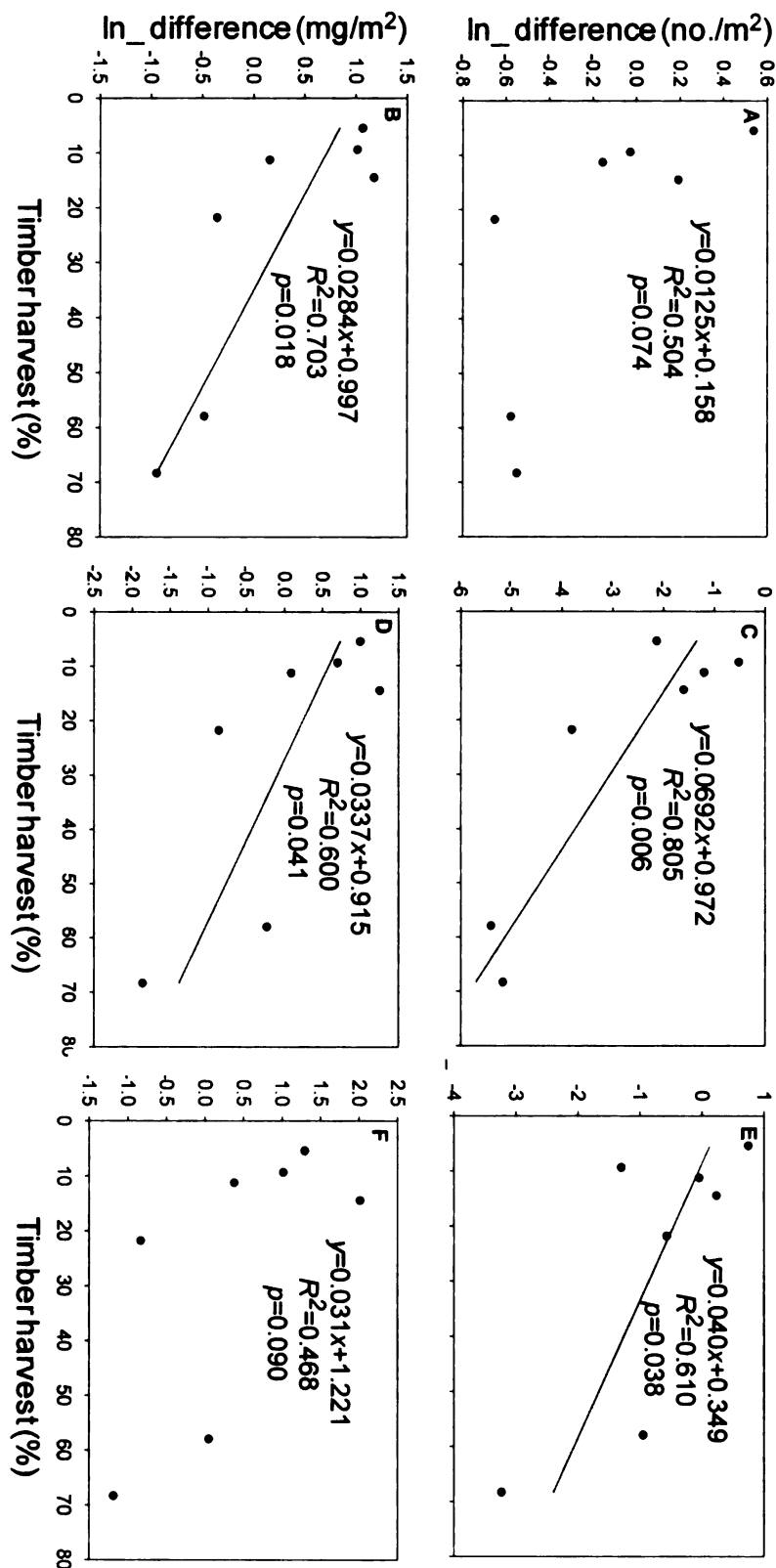


Table 2. Results of rmANCOVA analyzing the relationships between macroinvertebrate density, richness, insect biomass; biomasses of Diptera, Ephemeroptera, Plecoptera, collector-gatherers, scrapers, and predators with % timber harvest treated as a covariate during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>	<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>	<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>
<u>Density</u>											
Salmon	1, 6	1.05	0.346	<u>Diptera Biomass</u>				<u>Biomass</u>			
Timber Harvest	1, 68	0.11	0.746	Salmon	1, 6	1.26	0.305	Salmon	1, 6	0.76	0.417
Salmon x Timber				Timber Harvest	1, 68	0.07	0.787	Timber Harvest	1, 68	0.03	0.872
Harvest	1, 68	8.85	0.004	Salmon x Timber				Salmon x Timber			
				Harvest	1, 68	10.07	0.002	Harvest	1, 68	10.87	0.002
<u>Biomass</u>											
Salmon	1, 6	12.72	0.012	<u>Ephemeroptera</u>				<u>Scraper Biomass</u>			
Timber Harvest	1, 68	0.02	0.892	<u>Biomass</u>				Salmon	1, 6	3.26	0.121
Salmon x Timber				Salmon	1, 6	2.43	0.170	Timber Harvest	1, 68	0.51	0.478
Harvest	1, 68	14.68	<0.001	Timber Harvest	1, 68	0.31	0.577	Salmon x Timber	1, 68	3.76	0.057
				Salmon x Timber				Harvest			
				Harvest	1, 68	6.50	0.013				
<u>Richness</u>											
Salmon	1, 6	6.75	0.041	<u>Plecoptera</u>				<u>Predator Biomass</u>			
Timber Harvest	1, 68	0.88	0.353	<u>Biomass</u>				Salmon	1, 5	6.24	0.055
Salmon x Timber				Salmon	1, 6	11.78	0.014	Timber Harvest	1, 46	0.01	0.943
Harvest	1, 68	1.56	0.216	Timber Harvest	1, 68	0.17	0.683	Salmon x Timber	1, 46	1.48	0.229
				Salmon x Timber				Harvest			
				Harvest	1, 68	1.58	0.213				

Macroinvertebrate community structure

The NMDS ordination and MRPP revealed a significant ($T = 31.6$; $A = 0.08$; $p < 0.001$) difference in macroinvertebrate community structure before and during the salmon run (Fig. 5), but not among streams with different timber-harvest intensity. A total of 69% of the variation in macroinvertebrate community structure was explained by a three axes solution: 1st axis = 15.9%, 2nd = 13% and 3rd = 39.5%. Mean stress was 19.0 for the ordination and 26.3 for the Monte Carlo solution. Six taxa were considered significant indicators of macroinvertebrate communities before salmon spawning disturbance: *Epeorus longimanus* (Eaton) (Ephemeroptera: Heptageniidae, indicator value = 89%), Simuliidae (Diptera, 73%), Chironomidae (Diptera, 70%), *Baetis* (Ephemeroptera: Baetidae, 67%), *Suwallia* (Plecoptera: Chloroperlidae, 60%), and *Seratella tibialis* (McDunnough) (Ephemeroptera: Ephemerellidae, 57%) (Fig. 5). However, *Sweltsa* (Plecoptera: Chloroperlidae, 83%) was the only significant indicator taxon for communities sampled during the salmon run.

Figure 3. Linear regressions of the difference ('during salmon' - 'before salmon') of macroinvertebrate density (A), total insect biomass (B); and biomasses of Diptera (C), Ephemeroptera (D), gathering-collectors (E), and scrapers (F) regressed against sediment size.

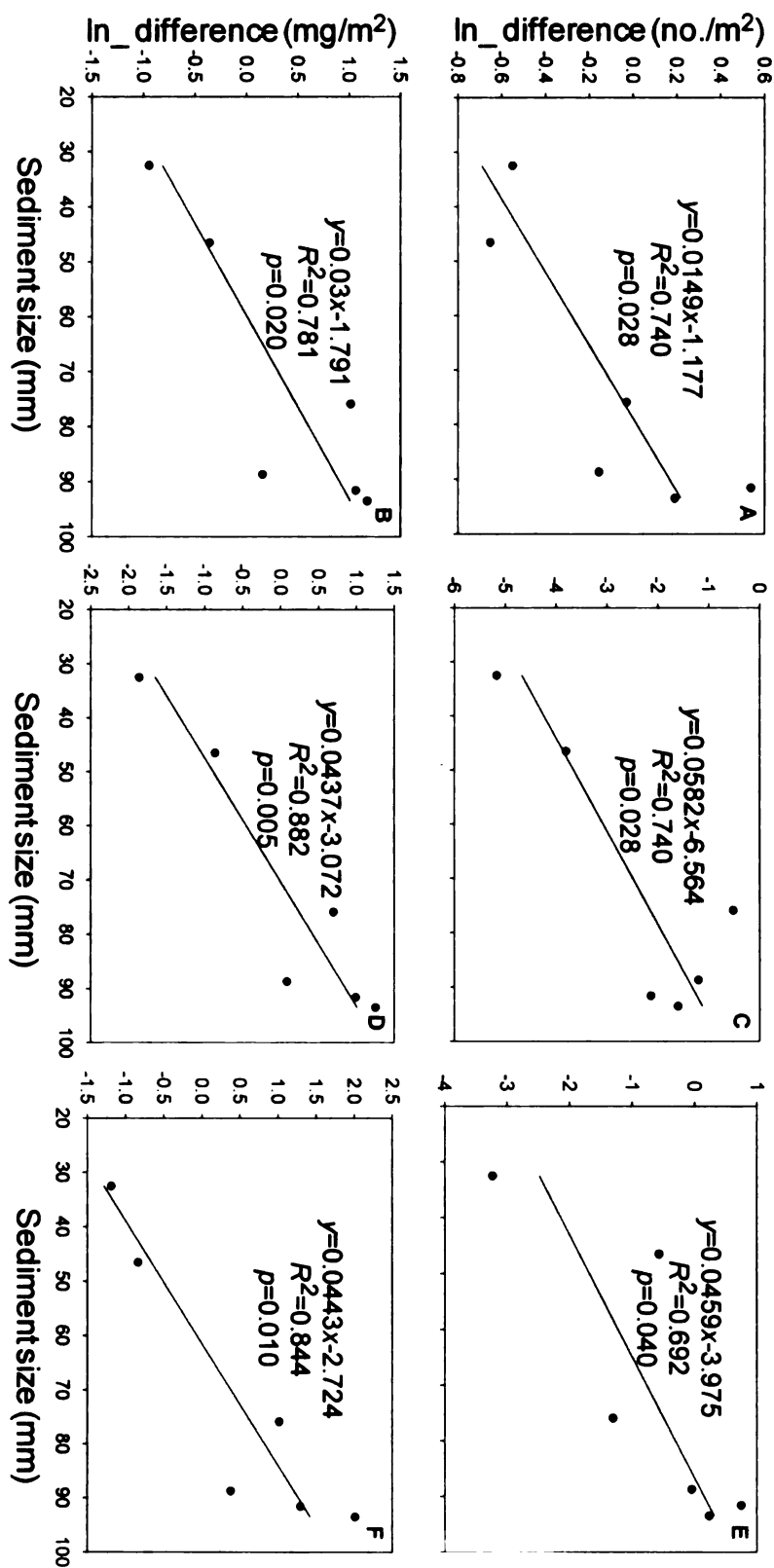


Table 3. Results of rmANCOVA analyzing the relationships between macroinvertebrate density, richness, insect biomass; biomasses of Diptera, Ephemeroptera, Plecoptera, collector-gatherers, scrapers, and predators with sediment size treated as a covariate during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>	<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>	<i>Effect</i>	<i>df</i>	<i>F</i>	<i>p-value</i>
<u>Density</u>											
Salmon	1, 5	9.64	0.027	<u>Diptera Biomass</u>				<u>Collector-gatherer</u>			
Sediment Size	1, 46	0.04	0.841	Salmon	1, 5	9.57	0.027	Salmon	1, 5	4.91	0.078
Salmon x Sediment Size	1, 46	0.04	0.841	Sediment Size	1, 46	0.05	0.832	Sediment Size	1, 46	0.03	0.867
				Salmon x Sediment Size	1, 46	4.31	0.043	Salmon x Sediment Size	1, 46	3.52	0.067
				Size				Size			
<u>Biomass</u>											
<u>Ephemeroptera Biomass</u>											
Salmon	1, 5	14.45	0.013	Salmon	1, 5	36.35	0.002	Salmon	1, 5	1	0.005
Sediment Size	1, 46	0.00	0.961	Sediment Size	1, 46	0.45	0.508	Sediment Size	1, 46	0.33	0.569
Salmon x Sediment Size	1, 46	21.76	<0.001	Salmon x Sediment Size	1, 46	37.70	<0.001	Salmon x Sediment Size	1, 46	6	<0.001
				Size				Size			
<u>Richness</u>											
Salmon	1, 5	14.26	0.013	<u>Plecoptera Biomass</u>				<u>Predator Biomass</u>			
Sediment Size	1, 46	1.52	0.223	Salmon	1, 5	0.60	0.474	Salmon	1, 5	0.05	0.828
Salmon x Sediment Size	1, 46	4.55	0.038	Sediment Size	1, 46	0.48	0.493	Sediment Size	1, 46	0.35	0.560
				Salmon x Sediment Size	1, 46	0.09	0.771	Salmon x Sediment Size	1, 46	0.12	0.732
				Size				Size			

Aquatic insect order-level responses

Diptera biomass was lower across all streams during the salmon run and a significantly greater spawning salmon disturbance effect was observed in streams with high timber harvest as compared to low timber harvest ($R^2=0.80$, $p=0.006$; Fig. 2C, Table 2 and 5). Salmon had a significantly greater disturbance effect on Diptera biomass in streams with finer sediments ($R^2=0.74$, $p=0.028$; Fig. 3C, Table 3) and less large wood ($R^2=0.71$, $p=0.035$; Fig. 4C, Table 4). Diptera biomass was dominated by the family Chironomidae (67%, of total Diptera) followed by the family Simuliidae (25%). Ephemeroptera biomass increased during the salmon run in streams with low timber harvest and decreased in streams with high timber harvest (Table 5). The magnitude of the disturbance effect increased with increasing timber harvest intensity ($R^2=0.60$, $p=0.041$; Fig. 2D, Table 2). We observed a greater disturbance effect on Ephemeroptera biomass in streams with finer sediments ($R^2=0.88$, $p=0.005$; Fig. 3D, Table 3) and low volumes of large wood ($R^2=0.72$, $p=0.031$; Fig. 4D). Ephemeroptera biomass consisted mostly of the family Heptageniidae (52%, of total Ephemeroptera), followed by the family Baetidae (28%). Plecoptera biomass was greater across all streams during the salmon run when timber harvest and large wood were treated as covariates ($p=0.014$; Table 2 and $p=0.013$; Table 4; respectively). Sediment size did not explain any of the variation in the response of Plecoptera biomass to salmon (Table 3). Plecoptera biomass was dominated by the family Chloroperlidae (90%, of total Plecoptera), followed by the family Nemouridae (5%).

Figure 4. Linear regressions of the difference ('during salmon' - 'before salmon') of macroinvertebrate density (A), total insect biomass (B); and biomasses of Diptera (C), Ephemeroptera (D), gathering-collectors (E), and scrapers (F) regressed against large wood volume.

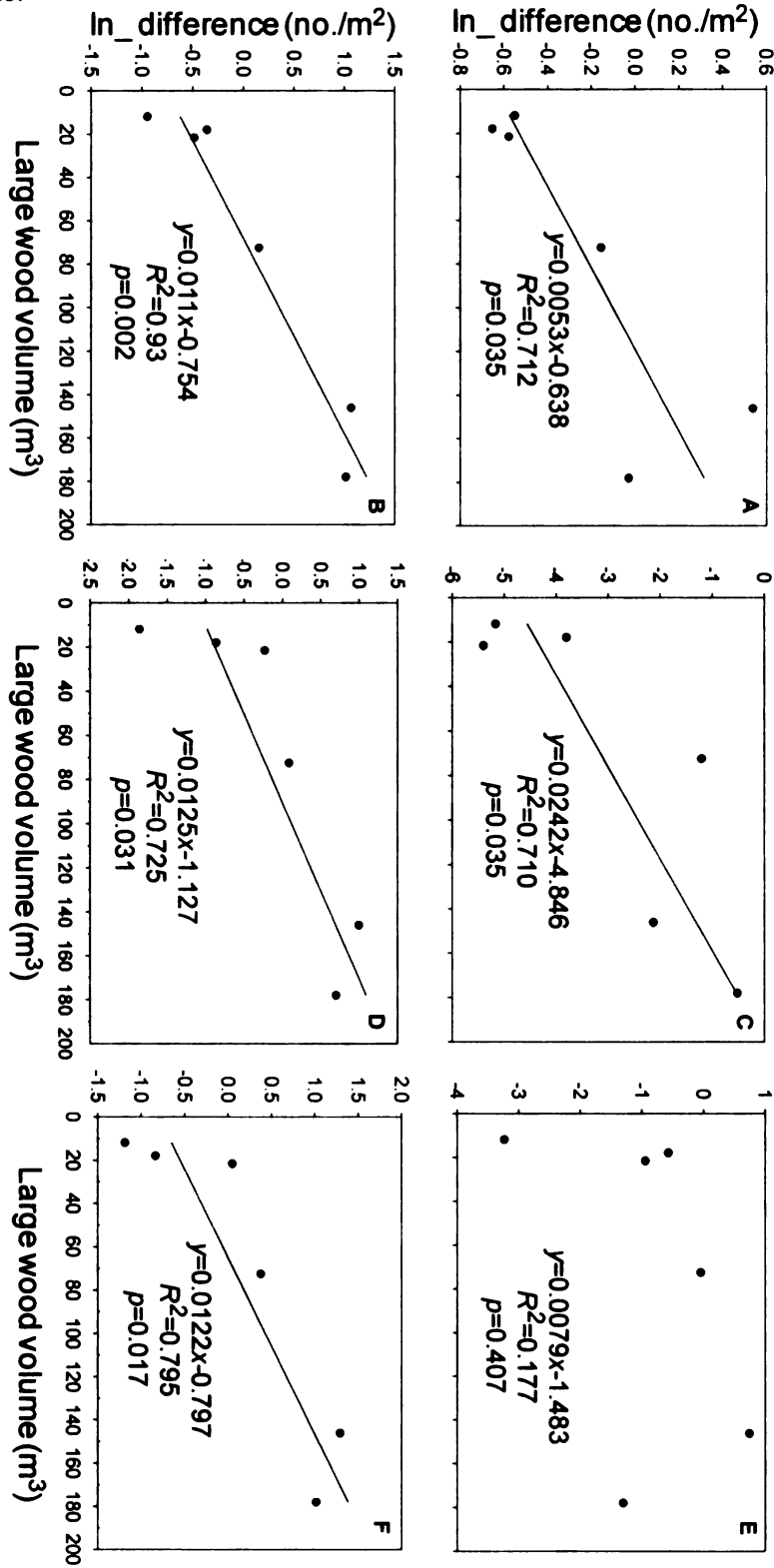


Table 4. Results of rmANCOVA analyzing the relationships between macroinvertebrate density, richness, insect biomass; biomasses of Diptera, Ephemeroptera, Plecoptera, collector-gatherers, scrapers, and predators with large woody debris (LWD) treated as a covariate during as compared to before the salmon run.

<u>Effect</u>	<u>df</u>	<u>F</u>	<u>p-value</u>	<u>Effect</u>	<u>df</u>	<u>F</u>	<u>p-value</u>	<u>Effect</u>	<u>df</u>	<u>F</u>	<u>p-value</u>
<u>Density</u>				<u>Diptera Biomass</u>				<u>Collector-gatherer Biomass</u>			
Salmon	1, 5	13.25	0.015	Salmon	1, 5	7.80	0.038	Salmon	1, 5	2.36	0.815
LWD	1,46	1.11	0.298	LWD	1,46	0.70	0.406	LWD	1,46	0.12	0.735
Salmon x LWD	1,46	8.94	0.005	Salmon x LWD	1,46	1.29	0.262	Salmon x LWD	1,46	0.61	0.438
<u>Biomass</u>				<u>Ephemeroptera Biomass</u>				<u>Scraper Biomass</u>			
Salmon	1, 5	13.85	0.014	Salmon	1, 5	8.53	0.033	Salmon	1, 5	5.54	0.065
LWD	1,46	0.61	0.437	LWD	1,46	1.13	0.294	LWD	1,46	1.31	0.258
Salmon x LWD	1,46	26.01	<0.001	Salmon x LWD	1,46	6.95	0.011	Salmon x LWD	1,46	7.79	0.008
<u>Richness</u>				<u>Plecoptera Biomass</u>				<u>Predator Biomass</u>			
Salmon	1, 5	51.42	<0.001	Salmon	1, 5	1.30	0.306	Salmon	1, 5	0.01	0.926
LWD	1,46	6.98	0.011	LWD	1,46	0.00	0.969	LWD	1,46	0.01	0.933
Salmon x LWD	1,46	7.66	0.008	Salmon x LWD	1,46	6.75	0.013	Salmon x LWD	1,46	4.92	0.032

Functional feeding group responses

The greatest disturbance effect on collector-gatherer biomass was observed in streams with high timber harvest as compared to streams with low harvest ($R^2=0.61$, $p=0.038$; Fig. 2E, Table 2 and 5). A significantly greater disturbance effect on collector-gatherer biomass was observed in streams with finer sediments as compared to streams with larger sediments ($R^2=0.69$, $p=0.04$; Fig. 3E, Table 3). Large wood volume was not an important covariate in collector-gatherer biomass response to salmon (Table 4) and no correlation was found between the disturbance effect on collector-gatherer biomass and large wood (Fig. 4E).

A greater salmon disturbance effect on scraper biomass was observed in streams with finer sediments ($R^2=0.84$, $p=0.01$; Fig. 3F, Table 3) and low volumes of large wood ($R^2=0.79$, $p=0.01$; Fig. 4F, Table 4). Timber harvest and sediment size did not explain any of the variation in predator biomass (Table 2). Large wood however was an important covariate for predator biomass as indicated by the significant salmon-timber harvest interaction ($p=0.032$, Table 4).

Figure 5 Non-Metric Multi Dimensional Scaling ordination showing the separation of macroinvertebrate community structure before and during the salmon run.

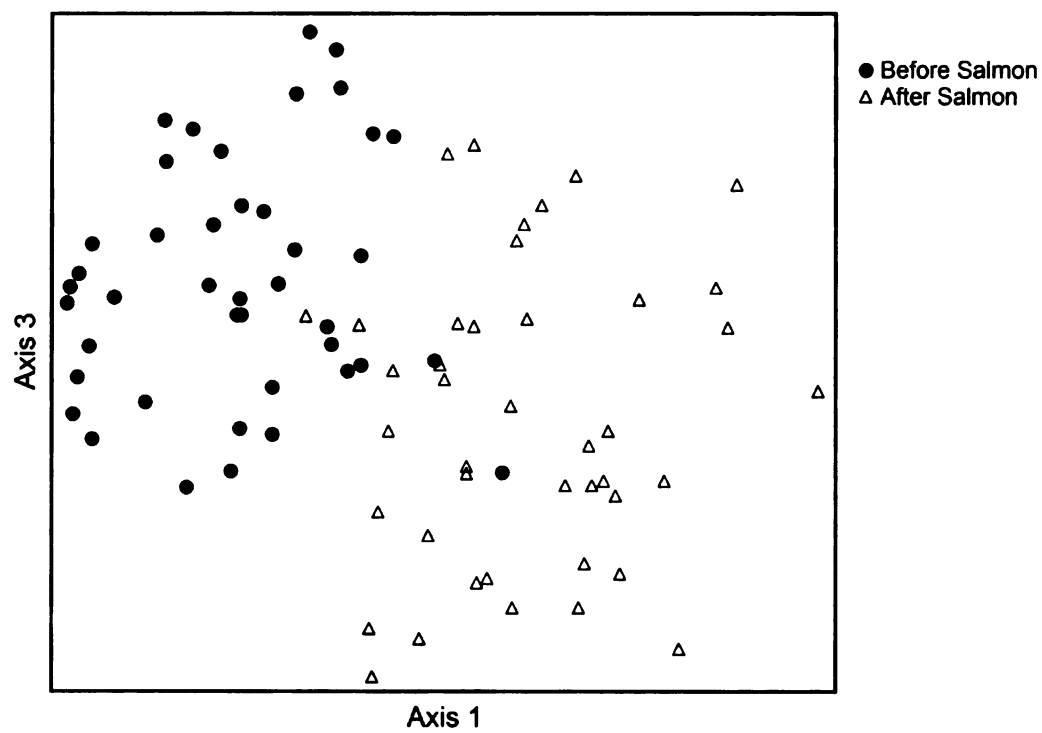


Table 5. Actual difference ('during salmon' – 'before salmon') of macroinvertebrate density (no./m²), insect biomass (mg/m²), richness; and biomasses (mg/m²) of Diptera, Ephemeroptera, Plecoptera, gathering-collectors, scrapers, and predators.

Stream	% Harvest	Density	Biomass	Richness	Diptera	Ephemeroptera	Plecoptera	Gatherers	Scrapers	Predators
Nossuk	5.42	931.33	1045.25	-47.17	-21.29	728.89	364.03	94.7	702.24	273.68
Indian	9.33	-51.83	791.8	4.83	-24.37	334.93	527.3	-84.98	396.9	567.45
Trocadero	11.22	-76.12	36.32	-47.16	-1.82	16.85	20.52	-0.66	56.02	-18.76
Dog Salmon	14.44	278.59	1124.96	-22.5	-32.26	993.86	149.92	37.54	1057.49	70.17
Maybeso	21.77	-612.24	-163.43	-77.67	-41.6	-273.5	135.1	-13.71	-252.14	97.69
Slide	57.91	-338.52	-185.42	-53.16	-163.25	-58.41	21.71	-54.82	9.53	-112.69
Twelve Mile	68.3	-884.36	-829.86	-63.5	-61.51	-983.97	216.18	-355.8	-389.36	-37.74

Discussion

Macroinvertebrate responses to salmon

Pacific salmon are considered to be ecosystem engineers because they modulate resource availability and reallocate biotic and abiotic materials (Jones et al. 1994). Upon the arrival of spawning salmon, I documented changes in macroinvertebrate community structure, richness, density, and biomass. Several studies in Alaska streams have documented reductions in macroinvertebrate density and alterations to benthic macroinvertebrate community organization during salmon spawning (Moore et al. 2004, Lessard and Merritt 2006, Moore and Schindler 2008, Monaghan and Milner 2009). I observed lower macroinvertebrate richness during the salmon run across all streams. Studies in New Zealand and Michigan streams also showed that spawning salmon reduce benthic macroinvertebrate richness (Hildebrand 1971, Field-Dodgson 1987), thereby having a negative impact on stream assemblages. This response is likely due to the large number of invertebrate taxa unable to survive the intense bioturbation impacts from salmon during migration and spawning activities (see also Janetski et al. 2009).

I found that taxonomic groups responded differently to salmon spawning. Diptera biomass was lower across all streams during the salmon run and the magnitude of this effect was greatest in streams with high timber harvest. Chironomidae were the dominant family in this order, comprising 70% of the biomass of all dipteran larvae collected. Other studies in Alaska streams have observed declines in Chironomidae density and biomass during salmon spawning (Peterson and Foote 2000, Moore et al. 2004, Lessard et al. 2009). Ephemeroptera biomass consisted mostly (52%) of heptageniid mayflies, which declined during the salmon run in streams with high timber harvest and increased

in streams with low harvest. Most genera in the family Heptageniidae are scrapers and several taxa such as *E. longimanus*, *Rhithrogena* (Ephemeroptera: Heptageniidae), and *Cinygmula* (Ephemeroptera: Heptageniidae) dominated before salmon, but then were less abundant during the salmon run. This response is most likely due to their feeding behavior, as these scrapers forage on biofilm from the tops of rocks in the active channel where redd construction is prevalent and thus are highly vulnerable to bioturbation impacts. In addition, biofilm is generally reduced in the main channel of these salmon streams during spawning (Janetski et al. 2009), a result also found in these same 7 streams in 2006 (Tiegs et. al 2008). Other mayfly taxa highly affected by salmon spawning were *Baetis*, *S. tibialis*, *Drunella grandis* (Eaton) (Ephemeroptera: Ephemerellidae) and *Drunella doddsi* (Needham) (Ephemeroptera: Ephemerellidae), consistent with others from Southeast Alaska that found significant declines in these taxa during the salmon run (Lessard and Merritt 2006, Lessard et al. 2009). Plecoptera density and biomass increased during the salmon run across all streams, mainly predaceous *Sweltsa* and *Suwallia*, which may consume the abundant salmon tissues and salmon eggs (Ellis 1970).

Multivariate ordination demonstrated significant separation of communities before and during the salmon run, with several taxa characterizing macroinvertebrate communities before the arrival of salmon and *Sweltsa* as the only significant indicator of communities associated with spawning activity. This result explains the significant decline in richness of riffle macroinvertebrates with the arrival of salmon, and suggests that sensitive taxa are unable to survive the massive bioturbation impacts due to salmon. Disturbance intolerant taxa may also actively move to refugia habitats such as backwater

pools or stream edges during bioturbation impacts. It is possible; however, that this separation may be due to evolved phenologies that are timed around the annual fall salmon run or macroinvertebrates. For example, some predatory taxa such as *Dicranota* (Diptera: Tipulidae) and *Sweltsa* were more abundant during salmon spawning and may be adapted to feeding on salmon tissues and eggs (Ellis 1970). Other shredder species, such as *Zapada cinctipes* (Banks) (Plecoptera: Nemouridae), could time their life histories around leaf litter input that occurs concomitantly with the salmon run. Lessard and Merritt (2006) reported that *Z. cinctipes* proliferated during the salmon run and speculated that they may benefit from both salmon nutrients and leaf litter inputs in late summer and fall. Some dipteran families, such as Chironomidae and Simuliidae, and ephemeropteran families, such as Heptageniidae and Baetidae, may time their life histories to avoid spawning salmon by emerging before the arrival of salmon (Moore and Schindler 2008, Lessard et al. 2009). The emergence of certain sensitive taxa before the salmon run may be evolutionarily favored by the historical legacy of thousands of years of spawning salmon disturbance. However, mechanistic experiments and longer-term data are needed to resolve these potential mechanisms.

Macroinvertebrate response to salmon and timber harvest interactions

The greatest reduction in macroinvertebrate density and insect biomass during the salmon run was observed in streams with high timber harvest as compared to less-impacted streams. In low harvest streams, macroinvertebrate density and biomass increased during the salmon run, consistent with responses in benthic algae in these same streams (Tiegs et al. 2008). In high-harvest streams, algal biomass and chlorophyll *a* declined during the salmon run but increased in more pristine streams. My results for

macroinvertebrate communities also suggest that the ecological role of salmon can be modified by stream structure in response to human disturbance.

Tiegs et al. (2008) documented that sediment size in our study streams was negatively related to percent timber harvest in the watershed. Other studies have shown similar patterns in other watersheds (Barr and Swanston 1970, Hawkins 1982, Murphy and Milner 1996, Dupuis and Stevenson 1999, Jones et al. 1999). Such shifts to finer sediments can have several deleterious effects on macroinvertebrate habitats, such as filling in interstitial hyporheic habitats, increasing abrasion and scour, and altering food web dynamics by influencing primary production (Allan 2004). The greatest decline in macroinvertebrate density and biomass occurred in streams with finer sediments, perhaps because smaller sediments are more readily dislodged by spawning salmon. For example, meta-analysis showed that the effect of salmon on macroinvertebrates was positive in streams with large sediments (>32 mm), but negative in streams with small sediments (<32 mm; Janetski et al. 2009). In my study, all streams had mean sediment sizes greater than 32 mm and yet we still observed a similar trend where salmon had a negative effect on macroinvertebrates in streams with small sediments and a positive effect in streams with larger sediments.

Reductions in regionally-important collector-gatherers (Cushing et al. 1995) in managed streams during salmon spawning could affect the secondary production of these streams and thus alter food web dynamics. The 3 dominant collector-gatherers in my streams were the mayflies *Baetis* and *S. tibialis*, and the flatworm *Planaria* (Seriata: Planariidae). Salmon redd construction in harvested streams may increase the mortality of collector-gatherers due to very fine sediments that may smash them by substrate

mobilized by salmon, or force them into stream drift. Collector-gatherers typically scavenge for food resources in benthic interstices and it is also likely that the finer sediments in high harvest streams may fill in these areas during salmon spawning and interfere with feeding. Scraping macroinvertebrates also were significantly affected by the interaction of salmon and timber harvest, with the greatest decline in scraper biomass observed in the high-harvest streams with small sediment sizes. The 3 dominant scraper macroinvertebrates in our streams were the mayflies *Cinygmula* and *E. longimanus*, and the caddisfly *Glossosoma* (Trichoptera: Glossosomatidae). Scrapers were perhaps the most vulnerable functional feeding group affected by spawning salmon as they typically scrape biofilm directly from the tops of rocks in the main channel where disturbance effects are likely to be greatest.

The volume of large wood was negatively related to percent watershed harvest, which has also been documented in other studies (Gregory et al. 1991, Montgomery and MacDonald 2002). Reductions in large wood can directly affect stream organisms by: 1) diminishing substrate for cover, attachment, and feeding (Ehrman and Lamberti 1992); 2) reducing shade and increasing stream temperatures (Bourque and Pomeroy 2001); and 3) altering flow dynamics, which effects both habitat distribution and heterogeneity (Allan 2004). The change in insect biomass over time was positively related to the volume of large wood with the greatest declines observed in streams with the lowest volume of large wood. This finding could be due to reduced habitat heterogeneity, which may limit the refugia available to insects and other macroinvertebrates during spawning periods. The abundance and diversity of macroinvertebrates, which are a major food resource for

juvenile salmonids, often increase with habitat complexity (Crowder and Cooper 1982, Robson and Barmuta 1998, Taniguchi and Tokeshi 2004).

Conclusions

In the relatively pristine streams, biomasses of scrapers, predators, collector-gatherers, and Ephemeroptera increased during salmon spawning whereas they declined in more harvested streams. The increased retentive capacity of salmon nutrients in complex pristine streams may allow for salmon nutrients to be more fully incorporated by the stream food web. Pristine streams may also provide macroinvertebrates with greater habitat diversity and more refugia, such as backwater pools, to buffer disturbance effects, as also observed in other non-salmon studies (Death and Winterbourn 1995, Gjerløv et al. 2003). Backwater pools are also more prevalent in pristine streams and may be important refuge habitats for fish such as overwintering salmonids (Heifetz et al. 1986). Greater channel complexity can also positively influence benthic algal production during annual salmon runs in Southeast Alaska (Tiegs et al. 2008).

My study is the first to explicitly examine combined salmon and timber harvest impacts on stream macroinvertebrate communities. As such, this study represents an important step toward understanding these interactive effects on macroinvertebrate communities and potentially salmon populations. Overall, the greatest salmon-induced reductions in macroinvertebrate density and insect biomass were observed in streams with a high degree of timber harvest, small sediments, and low volumes of large wood. Timber harvest operates through multiple mechanisms to reduce channel complexity and thereby modify the effect that spawning salmon have on benthic communities. I

demonstrate that changes at the watershed level due to timber harvest can amplify local disturbances from spawning salmon and elicit declines in macroinvertebrate density and biomass, potentially altering the productivity of stream food webs.

Chapter 2. Macroinvertebrates Utilize Refugia in Response to Spawning Salmon Disturbance in Southeast Alaskan streams

Abstract

Spawning salmon create patches of disturbance through redd digging and upstream migration which can alter the abundance and community structure of macroinvertebrate communities. We investigated how the presence of salmon spawners alter the distribution, abundance, and community composition of macroinvertebrates among habitats with different degrees of spawning disturbance activity including riffles, backwater pools, the hyporheic zone, and edge habitats, as well as stream drift in Twelve Mile Creek on Prince of Wales Island, Alaska, USA. We predicted that spawning salmon would 1) reduce the abundance and richness of macroinvertebrates in riffles; 2) increase macroinvertebrate abundance and richness in backwater pool, stream edge, and hyporheic zone refuge habitats during the salmon run; and 3) increase the magnitude of stream drift. We quantitatively sampled benthic macroinvertebrates from the four benthic habitats and collected 30 min drift samples six times before and four times during the salmon run. Spawning salmon significantly reduced the density ($p < 0.001$), biomass ($p < 0.001$), and richness ($p = 0.009$) of macroinvertebrates occurring in riffle habitats compared to before the run. Within backwater pools, most taxa declined during spawning, especially the Limnephilidae (Trichoptera), but *Chironomus* (Diptera: Chironomidae) and *Sweltsa* (Plecoptera: Chloroperlidae) densities increased during spawning. Stream edges appeared to offer refugia for certain taxa such as Limnephilidae, Ostracoda, Simuliidae (Diptera), and *Sweltsa* stoneflies. The hyporheic zone appeared to offer refugia for certain invertebrate taxa including *Chironomus*, *planaria* flatworms, Apatanidae

(Trichoptera) and Limnephilidae, and overall insect density increased in the hyporheos during salmon spawning. Macroinvertebrate density ($p=0.05$) and richness ($p=0.001$) increased in stream drift during salmon spawning. This research elucidated some of the mechanisms of benthic macroinvertebrate persistence despite massive annual main-channel benthic disturbance by spawning salmon. Biomonitoring and other benthic studies should include sampling from several habitat types to provide more comprehensive information on how macroinvertebrates respond to salmon disturbance. Habitat heterogeneity offers refugia for macroinvertebrates and may be a crucial determinant of macroinvertebrate survivability during salmon spawning.

Introduction

Spawning salmon have been documented to induce massive physical disturbance reported to redistribute of benthic substrates during upstream migration and redd construction (Duncan and Brusven 1985, Minakawa and Gara 2003, Tiegs et al. 2008, 2009, Monaghan and Milner 2009). Spawning disturbance can play a critical role in influencing nutrient transfer and nutrient availability to benthic communities (Moore and Schindler 2008, Monaghan and Milner 2009). Benthic disturbances from spawning salmon can alter the distribution, abundance, and community composition of benthic organisms and cause significant reductions of macroinvertebrates in riffle habitats where salmon activities are often greatest (Peterson and Foote 2000, Chaloner et al. 2004, Moore et al. 2004, Lessard et al. 2009). Not all benthic habitats are equally impacted by spawning salmon. The most common areas for spawning activities are main-channel riffle and run habitats, and areas that receive less impact by spawners are stream edges

which are too shallow for redd construction, and backwater pools or other slack water habitats that do not offer sufficient oxygen important to salmon egg survival (Quinn 2005). Macroinvertebrates may utilize these less impacted habitats as refugia to avoid bioturbation impacts during periods of intense salmon spawning (Minakawa and Gara 2003).

Habitat heterogeneity is important for stream biota as it offers diverse habitat types that sustain diverse and unique taxa (Kerans and Karr 1992, Gjerløv et al 2003). For example, riffle habitats are often dominated by scrapers, such as heptageniid mayflies, that feed on abundant biofilm within riffles and collector-filterers, such as simuliid dipterans, that collect fine particulate organic matter from stream drift. Backwater pools typically sustain shredders, such as limnephilid case-building caddisflies, and collector gatherers, such as some genera of the family Chironomidae (Merritt et al. 2008). Backwater pools represent important reach scale heterogeneity in stream flow and substrate composition, which may offer efficacy as refugia for macroinvertebrates and other stream organisms (Lancaster 1993). During salmon spawning, macroinvertebrates in highly-disturbed riffle habitats may migrate, or be displaced, into low-disturbance habitats such as backwater pools, stream edges, or the hyporheic zone. These habitats could be important for the completion of growth and development of certain species that would otherwise be continually displaced downstream resulting in increased mortality.

Habitat refugia can be defined as distinct habitats that sustain communities that do not normally become disturbed, or display resilience to disturbances (Sedell et al. 1990, Winterbottom et al. 1997). Biota that are transient or different than the typical

communities may inhabit refugia as they move in from disturbed areas (Sedell et al. 1990). Stream edges may offer refuge to macroinvertebrates during flood events (Negishi et al. 2002) and possibly during salmon spawning as edges are areas of the stream channel that receive less salmon spawning activity compared to main-channel riffles where disturbance is often greatest. The hyporheic zone is recognized as an important refugium for aquatic macroinvertebrates and other river organisms during hydrological disturbances, such as floods or droughts (Williams and Hynes 1974, Oliver et al. 1997, Rosario 2000), and may also offer macroinvertebrates refuge in response to spawning salmon disturbance.

Spawning-related fluctuations in benthic topography and community structure are a form of substrate disruption which likely increases invertebrate drift (Waters 1972). Much research has been done concerning the three different types of macroinvertebrate drift: 1) constant (casual) drift; 2) behavioral (predictable) drift; and 3) catastrophic (sudden) drift that is most often a response to physical or chemical factors (Waters 1972, Hynes 1975, Chutter 1975, Waters and Hokenstrom 1980). Spawning salmon can cause catastrophic drift of macroinvertebrates due to bioturbation impacts (Peterson and Foote 2000), or salmon can cause behavioral drift if benthic macroinvertebrates have evolved life history traits to drift in avoidance of spawning disturbance due to thousands of years of exposure to annual salmon runs. Most research regarding macroinvertebrate drift and fish populations has focused on predation pressures as the causal mechanism for increased drift (Ringler 1983, Skinner 1985, Bowles et al. 1988). Few studies have tested the effect of spawning salmon disturbance as a means of dislodgement potentially increasing the magnitude of macroinvertebrate drift (see Peterson and Foote 2000,

Minakawa and Gara 2003). Macroinvertebrates that are dislodged into stream drift may be displaced into slow moving waters such as stream edges or backwater pools, or they may actively move into edges, pools, or the hyporheic zone to avoid bioturbation impacts after resettlement in runs or riffles.

This research quantified macroinvertebrate community composition throughout a salmon run evaluating temporal shifts in community composition among four in-stream habitats. We investigated how the presence of salmon spawners altered the differential distribution, abundance, and community composition of macroinvertebrates among riffles, backwater pools, the hyporheic zone, and edge habitats, as well as stream drift. We hypothesized that spawning salmon would: 1) reduce the abundance and richness of macroinvertebrates in riffles; 2) increase macroinvertebrate abundance and richness in backwater pool, stream edge, and hyporheic zone refuge habitats during the salmon run; and 3) increase the magnitude of macroinvertebrates in stream drift.

Materials and Methods

Study Sites

This study was conducted between June and September 2008 within a 300 meter reach of Twelve Mile Creek on Prince of Wales Island within the Tongass National Forest, Southeast Alaska, USA. Prince of Wales Island has a maritime climate with a mean annual precipitation of 25cm and a mean air temperature of 7 °C (U.S. Department of Agriculture, Forest Service 1997). Watersheds on Prince of Wales Island are composed of coniferous temperate rainforest that has been primarily managed for timber harvest and Twelve Mile Creek has had 68% of its watershed harvested for timber.

Dominant riparian tree species of the stream include: red alder (*Alnus rubra* (Bong)), western hemlock (*Tsuga heterophylla* (Rafinesque)), and Sitka spruce (*Picea sitchensis* (Bongard)). Biotic and abiotic characteristics of Twelve Mile Creek are listed in Table 6.

Table 6. Characteristics of riffle, stream edge, and backwater pool habitats in Twelve Mile Creek, Southeast Alaska, USA. Numbers in parenthesis represent standard errors.

Habitat	Average Area (m ²)	Temperature (°C)	% DO	SPC	pH	Mean Sediment Size (mm)	Mean Chlorophyll <i>a</i> (mg/m ²)	
							Before Salmon	During Salmon
Riffle	185.22 (0.25)	9.69 (0.09)	99.18 (0.54)	147.82 (0.2)	8.14 (0.02)	30.92 (3.03)	19 (5.79)	8.44 (1.22)
Edge	N/A	10.84 (0.54)	97.88 (0.85)	145.36 (1.38)	8.07 (0.06)	21.95 (5.10)	25.5 (7.04)	10.1 (1.8)
Pool	35.53 (0.23)	9.79 (0.16)	85.33 (9.7)	141.78 (4.27)	7.82 (0.2)	23.78 (3.49)	68.7 (12.39)	14.88 (1.78)
								10.29 (1.08)

Macroinvertebrate Sampling and Processing

Macroinvertebrate samples were collected from 5 replicate riffles, backwater pools, stream edges, and hyporheic wells every 10 days from 27 June until 20 September 2008, for a total of 10 sampling dates, 6 pre-salmon and 4 during salmon sampling dates. There was a substantial flood that prevented sampling on 23 August which resulted in 10 instead of 11 sampling dates. For riffles, backwater pools, and stream edges, benthic macroinvertebrates were collected quantitatively using a large PVC tube with a diameter of 36cm and an area of 0.4m^2 . The tube was sealed within the benthic sediments so that there was no water movement from outside the tube. Samples were collected by swirling and mixing the benthos within the tube at a depth of 8cm for 30s. A 1mm mesh net was then used to scoop up large organic matter and macroinvertebrates for 30s, followed by mixing for 30s, and then scooping again with a 250 μm mesh net for another 30s to collect smaller pieces of organic matter and macroinvertebrates (Fig 6). The collected materials were rinsed through a 250 μm sieve, placed in plastic bags and preserved in 70% ethanol for later processing. We defined the edge of a stream as the low-velocity area along the wetted stream bank that was 1/10 the width of the entire stream channel. Backwater pools were defined as low-velocity areas lateral to the stream channel that were connected to the main channel at low flow, caused by large wood debris or boulders, and were of suitable depth (no deeper than 70 cm) to allow for macroinvertebrate sampling.

Hyporheic macroinvertebrates were collected using 60 cm long hyporheic wells installed 30 cm into the stream bottom at randomly selected areas within each riffle. All wells were capped to avoid surface and water column invertebrates from getting into the wells. The bottom 15cm of the wells had 40 small holes (5mm diameter) drilled into the

sides to allow invertebrates to be pulled from a larger volume of water surrounding the bottom of the wells. A bilge pump was used to pump 2 liters of hyporheic water and invertebrates per sample (Fig 7). Hyporheic water was then rinsed through a 250 μ m sieve, placed in plastic bags and preserved in 70% ethanol for later processing.

Macroinvertebrate drift was collected by placing three 250 μ m drift nets evenly spaced across the channel and perpendicular to stream flow at noon once every 10 days from June thru September corresponding to benthic habitat sampling dates (Fig 8). We elevated nets 3cm above the sediment to avoid collecting benthic invertebrates that were not part of the drift. Drift nets were left out for 30 minutes and discharge was measured in front of each net. After 30 minutes, the nets were rinsed; the collected materials put through a 250 μ m sieve, placed in plastic bags, and preserved in 70% ethanol for later processing. Macroinvertebrates were counted and identified to the lowest reliable taxon: insects were identified to genus or species (except the Chironomidae which were left at family), and non-insects were identified to class or order. Insect taxa also were measured for total length (nearest 0.5 mm) to estimate biomass based on published length-mass relationships (Benke et al. 1999).

Habitat characteristics

Late-summer salmon runs were dominated by pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*). Salmon were quantified in 4 meter wide belt transects perpendicular to stream flow every 10 m for the entire 300 m reach. These counts were then scaled up to estimate the number of salmon present in the 300 m stream reach on each date (Tiegs et al. 2009). Salmon were counted from the start of the

spawning run and approximately weekly for the duration of the run until mostly carcasses remained in the streams.

In each habitat we measured pH, % dissolved oxygen, and conductivity using a Hydrolab MS-5 Mini-Sonde, habitat area, % canopy cover using a spherical densiometer, sediment size using a Wentworth scale gravelometer, water velocity using a digital flow meter, and water depth using a meter stick (Table 1). These measures were taken at three different times throughout the study. To establish in-habitat autochthonous production we measured benthic biomass (as chlorophyll *a*) four times over the course of the study. Three rocks were randomly selected from each habitat, placed in plastic bags, and brought back to the lab for processing. In the lab, rocks were scraped entirely with a bristled brush and then filtered onto pre-ashed glass fiber filters with a SA55NXGTE-4870 Filtering Tower and chlorophyll *a* measured with a Trilogy Turner Design Fluorometer.

Fig 6. PVC tube, 1mm mesh net scooper and 250 μ m mesh net scooper used to collect benthic macroinvertebrate samples.

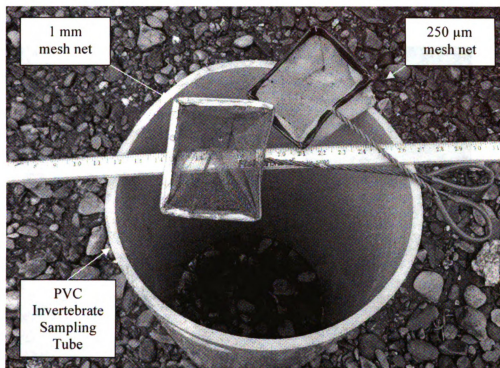


Fig 7. Macroinvertebrates sampling from the hyporheic zone with a bilge pump.



Fig 8. Drift nets used to collect drifting macroinvertebrates.



Statistical Analysis

A repeated measures analysis of variance (rmANOVA) was performed to determine whether salmon presence altered macroinvertebrate abundance and taxa composition. The two factors were salmon and habitat, salmon (before versus during) was treated as the repeated factor, and habitat number (replicates of each habitat) were treated as random effects, and compound symmetric covariance structure was specified using SAS (Version 11; SAS Institute, Cary, North Carolina, USA). There were $n=6$

before salmon sampling dates, and $n=4$ during salmon sampling dates, and a total of 230 samples were collected. Macroinvertebrate response variables were density, total biomass, richness; and the biomasses of Ephemeroptera, Plecoptera, Trichoptera, Diptera, shredders, collector-gatherers, collector-filterers, scrapers, predators and biomass of the 7 most dominant taxa: *Chironomus*, *Sweltsa*, *Ameletus*, *Baetis*, *Cinygmula*, and *Suwallia*. Results were considered significant when $p<0.05$. ANOVA assumptions were evaluated from normal probability plots, Shapiro-Wilk test statistics, and residual plots; natural logarithmic transformations or transformations to the power of 2 or 3 were used to correct violations. All macroinvertebrate response variables were plotted as bar charts before and during the salmon run using Sigma Plot (version 11; Sigma Plot software, San Jose, California, USA) to establish changes in macroinvertebrate variables in relation to salmon presence.

Results

Macroinvertebrate density, biomass, and richness

Macroinvertebrate density significantly declined in riffles ($p<0.001$) during the salmon run, did not change in pool and edge habitats, and significantly increased in the hyporheic zone ($p=0.019$) and stream drift ($p=0.052$) during the salmon run (Fig 9A, Table 7). Insect biomass significantly decreased in riffles ($p<0.001$) and backwater pools ($p=0.002$) during the salmon run (Fig 9B, Table 7). There were non-significant increases in insect biomass within edge habitats and in drift and no changes in hyporheic habitats. Macroinvertebrate richness significantly decreased in riffle habitats ($p=0.009$), did not significantly change in pool and edge habitats, and significantly increased in stream drift

($p=0.001$) during salmon spawning (Fig 9C, Table 7). There was an increase in macroinvertebrate richness in the hyporheic zone during salmon spawning, though this was not statistically significant (Table 7).

Fig 9. Macroinvertebrate density (no./m²) (A), insect biomass (B), and macroinvertebrate richness (C) differences before and during the salmon run in stream edges, riffles, backwater pools, the hyporheic zone, and stream drift.

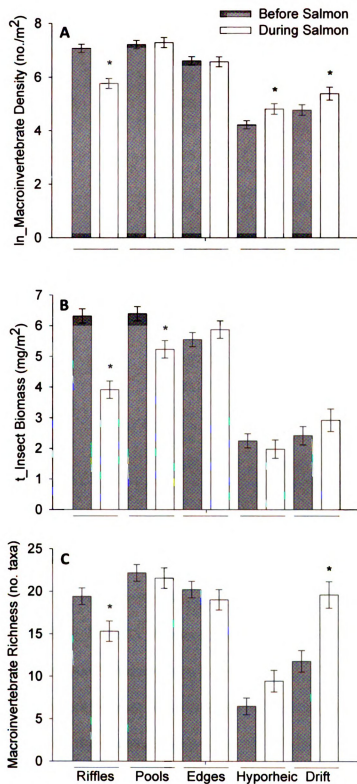


Table 7. Results of rmANOVA analyzing macroinvertebrate density, richness, and insect biomass during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F-value</i>	<i>P-value</i>
<u>Macroinvertebrate Density</u>			
Edge	1, 218	0.02	0.877
Riffle	1, 218	29.11	<0.001
Drift	1, 218	3.82	0.052
Pool	1, 218	0.09	0.766
Hyporheic	1, 218	5.55	0.019
<u>Insect Biomass</u>			
Edge	1, 218	0.79	0.376
Riffle	1, 218	43	<0.001
Drift	1, 218	1.14	0.287
Pool	1, 218	9.99	0.002
Hyporheic	1, 218	0.51	0.475
<u>Macroinvertebrate Richness</u>			
Edge	1, 218	0.59	0.442
Riffle	1, 218	6.92	0.009
Drift	1, 218	15.06	0.001
Pool	1, 218	0.16	0.693
Hyporheic	1, 218	3.42	0.066

Insect Order-Level Response to Spawning Salmon

Ephemeroptera biomass significantly decreased in riffle habitats ($p < 0.001$) during the salmon run but did not significantly change in any of the other habitats or stream drift during spawning (Fig 10A, Table 8). The most dominant mayfly families were: Heptageniidae (34%, of total Ephemeroptera larvae collected), Ameletidae (30%), and Baetidae (29%). Plecoptera biomass did not significantly change in any habitats during salmon spawning, though there was an appreciable yet non-significant increase in

plecopteran drift during salmon spawning (Fig 10B, Table 8). The most dominant plecopteran families were: Chloroperlidae (96%; of total Plecoptera larvae collected) and Leuctridae (1%). Trichoptera biomass did not change in riffle or pool habitats, significantly increased in stream edge habitats ($p=0.028$), did not change in hyporheic habitats, and significantly decreased in stream drift ($p=0.023$) during the salmon run (Fig 10C, Table 8). The most dominant caddisfly larvae were: Limnephilidae (61%; of total Trichoptera larvae collected) and Apataniidae (15%). Diptera biomass significantly decreased in riffles ($p<0.001$), did not change in pools, significantly decreased in edges ($p=0.042$) and did not change in the hyporheos or stream drift during salmon spawning (Fig 10D, Table 8). The most dominant fly families were: Chironomidae (82%; of total Diptera larvae collected) and Simuliidae (11%).

Fig 10. Ephemeroptera biomass (no./m²) (A), Plecoptera biomass (B), Trichoptera biomass (C), and Diptera Biomass (D) differences before and during the salmon run in stream edges, riffles, backwater pools, the hyporheic zone, and stream drift.

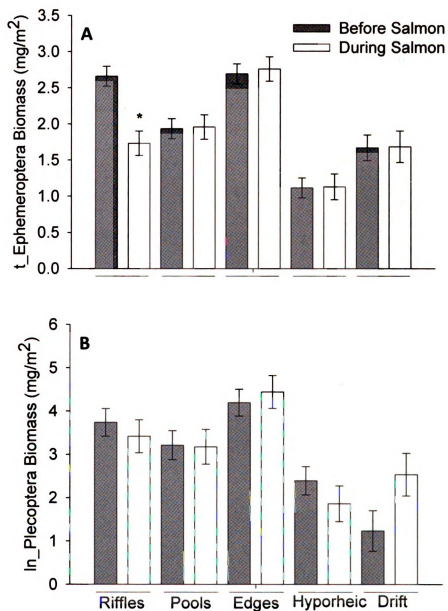


Fig 10. Continued

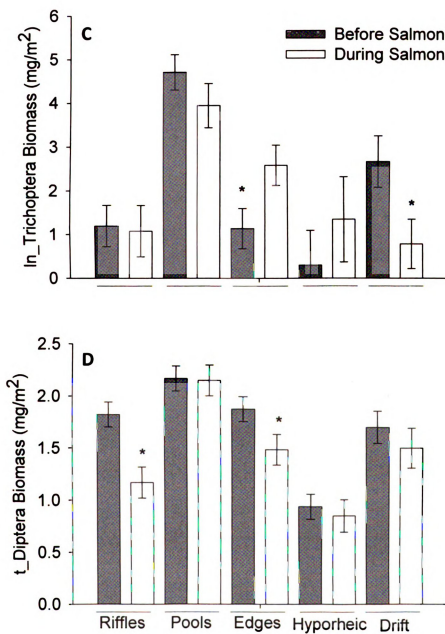


Table 8. Results of rmANOVA analyzing Ephemeroptera, Plecoptera, Trichoptera, and Diptera biomasses (mg/m^2) during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F-value</i>	<i>P-value</i>
<u>Ephemeroptera Biomass</u>			
Edge	1, 218	0.09	0.758
Riffle	1, 218	18.15	<0.001
Drift	1, 218	0	0.959
Pool	1, 218	0.01	0.918
Hyporheic	1, 218	0	0.946
<u>Plecoptera Biomass</u>			
Edge	1, 218	0.25	0.617
Riffle	1, 218	0.41	0.521
Drift	1, 218	3.65	0.057
Pool	1, 218	0.01	0.943
Hyporheic	1, 218	1.01	0.315
<u>Trichoptera Biomass</u>			
Edge	1, 218	4.96	0.028
Riffle	1, 218	0.02	0.875
Drift	1, 218	5.33	0.023
Pool	1, 218	1.39	0.241
Hyporheic	1, 218	0.69	0.408
<u>Diptera Biomass</u>			
Edge	1, 218	4.18	0.042
Riffle	1, 218	11.73	<0.001
Drift	1, 218	0.66	0.419
Pool	1, 218	0.01	0.925
Hyporheic	1, 218	0.2	0.653

Functional-Feeding Group Response to Spawning Salmon

Shredder biomass increased significantly in riffles ($p=0.023$), decreased significantly in pools ($p<0.001$), and did not change in edges, the hyporheos, or stream drift during the salmon run (Fig 11A, Table 9). The most dominant shredders were Limnephilidae (88%; of total shredder larvae collected) and Tipulidae (9%). Collector-gatherer biomass decreased significantly in riffles ($p<0.001$), did not change in pools and edges, increased significantly in the hyporheic zone ($p=0.034$), and did not change in stream drift during salmon spawning (Fig 11B, Table 9). The dominant collector-gatherers were *Chironomus* (32%; of total collector-gatherer larvae collected) and *Planaria* (12%). Collector-filterer biomass significantly decreased in riffles ($p<0.001$) and backwater pools ($p<0.001$), and did not significantly change in edges, the hyporheos, or stream drift during the salmon run (Fig 11C, Table 9). However, there was an appreciable, yet non-significant, increase in collector-filterer biomass in edge and hyporheic habitats during the salmon run (Fig 11C). The dominant collector-filterers in our samples were Simuliidae (73%; of total collector-filterer larvae collected) and Ostracoda (21%). Scraper biomass significantly decreased in riffle habitats ($p<0.001$) and did not show considerable changes in the other habitats or stream drift during salmon spawning (Fig 11D, Table 9). The dominant scrapers were Heptageniidae (84%; total scraper biomass collected) and Ameletidae (11%). Predator biomass significantly decreased in riffle habitats ($p=0.002$), did not significantly change in pools or edges, and significantly increased in stream drift ($p<0.001$) during the salmon run (Fig 11E, Table 9). The dominant predators in the stream were Chloroperlidae (94%; of total predator larvae collected) and Dytiscidae (3%).

Fig 11. Shredder biomass (mg/m^2) (A), Collector-gatherer biomass (B), Collector-filterer biomass (C), Scraper biomass (D), and Predator biomass (E) differences before and during the salmon run in stream edges, riffles, backwater pools, the hyporheic zone, and stream drift.

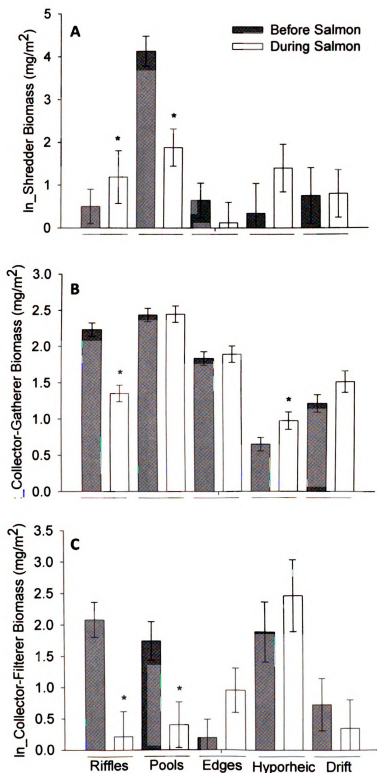


Fig 11. Continued

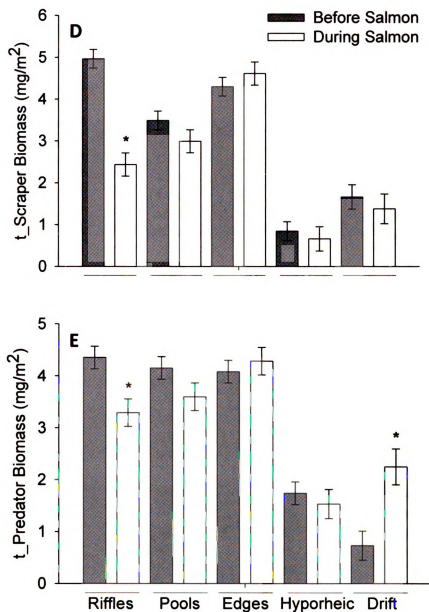


Table 9. Results of rmANOVA analyzing Shredder, Collector-gatherer, Collector-filterer, Scraper, and Predator biomasses (mg/m^2) during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F-value</i>	<i>P-value</i>
<u>Shredder Biomass</u>			
Edge	1, 218	1.5	0.222
Riffle	1, 218	5.27	0.023
Drift	1, 218	0	0.954
Pool	1, 218	16.28	<0.001
Hyporheic	1, 218	1.41	0.238
<u>Collector-gatherer Biomass</u>			
Edge	1, 218	0.16	0.687
Riffle	1, 218	36.13	<0.001
Drift	1, 218	2.41	0.122
Pool	1, 218	0	0.949
Hyporheic	1, 218	4.57	0.034
<u>Collector-filterer Biomass</u>			
Edge	1, 218	6.14	0.014
Riffle	1, 218	21.89	<0.001
Drift	1, 218	0.38	0.539
Pool	1, 218	21.11	<0.001
Hyporheic	1, 218	0.6	0.441
<u>Scraper Biomass</u>			
Edge	1, 218	0.78	0.377
Riffle	1, 218	50.71	<0.001
Drift	1, 218	0.39	0.535
Pool	1, 218	1.94	0.166
Hyporheic	1, 218	0.26	0.614
<u>Predator Biomass</u>			
Edge	1, 218	0.35	0.556
Riffle	1, 218	9.55	0.002
Drift	1, 218	11.7	<0.001
Pool	1, 218	2.6	0.108
Hyporheic	1, 218	0.34	0.563

Specific Taxa Responses to Spawning Salmon

The most dominant insect taxa (from most abundant to least abundant) were: *Chironomus* (Meigan) (Diptera: Chironomidae; 19.9%; of total taxa), *Sweltsa* (Yurock) (Plecoptera, Chloroperlidae; 7.6%), *Ameletus* (McDunnough) (Ephemeroptera: Heptageniidae; 5.6%), *Baetis* (Umpqua) (Ephemeroptera: Baetidae; 5.3%), *Cinygmula* (Dodds) (Ephemeroptera: Heptageniidae; 5.1%), and *Suwallia* (Ricker) (Plecoptera: Chloroperlidae; 3.2%). *Chironomus* biomass significantly declined in riffles ($p<0.001$) and pool ($p=0.014$), and significantly increased in the hyporheic zone ($p=0.002$) and drift ($p=0.024$) (Fig 12A, Table 10). *Sweltsa* were not present prior to salmon arrival and then significantly increased in all habitats ($p<0.001$) as well as stream drift ($p<0.001$) during the salmon run, and were most prominent in edge and riffle habitats (Fig 12B, Table 10). *Ameletus* biomass did not significantly change in any habitats or drift after the arrival of salmon (Fig 12C, Table 10). *Baetis* biomass significantly declined in riffles ($p<0.001$), did not change in pools, significantly declined in edges ($p<0.001$), and did not significantly change in the hyporheos or stream drift during salmon spawning (Fig 12D, Table 10). *Cinygmula* biomass significantly declined in riffles ($p<0.001$), did not change in pools, significantly declined in stream edges ($p=0.048$) and remained fairly low and uniform in the hyporheos and stream drift during spawning (Fig 12E, Table 10). *Suwallia* were present prior to salmon arrival and then significantly declined in riffles ($p<0.001$), pools ($p<0.001$), edges ($p<0.001$), the hyporheic zone ($p=0.004$), and did not significantly change in stream drift during spawning (Fig 12F, Table 10).

Fig 12. *Chironomus* biomass (mg/m^2) (A), *Sweltsa* biomass (B), *Ameletus* biomass (C), *Baetis* biomass (D), *Cinygmula* biomass (E), and *Suwallia* biomass (F) throughout the salmon run in stream edges, riffles, backwater pools, the hyporheic zone, and stream drift.

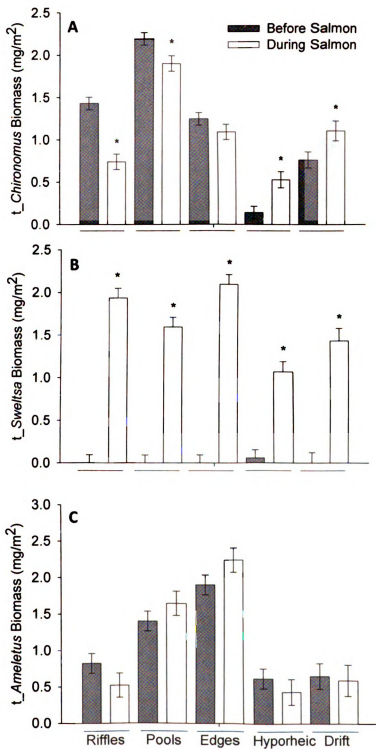


Fig 12. Continued

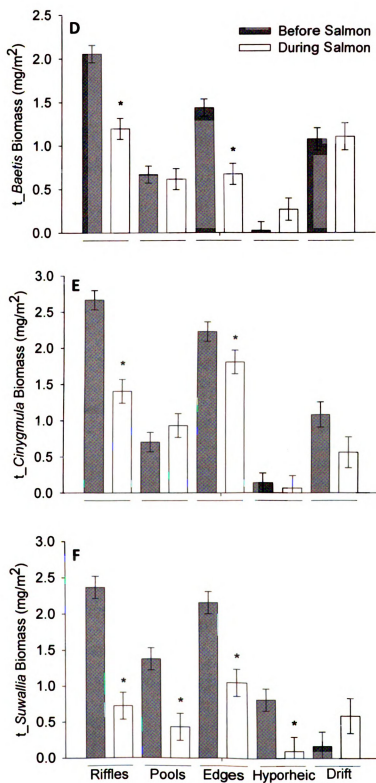


Table 10. Results of rmANOVA analyzing *Ameletus*, *Baetis*, *Cinygmula*, *Chironomus*, *Sweltsa*, and *Suwallia* biomass (mg/m²) during as compared to before the salmon run.

<i>Effect</i>	<i>df</i>	<i>F-value</i>	<i>P-value</i>
<u>Chironomus Biomass</u>			
Edge	1, 218	1.8	0.181
Riffle	1, 218	34.7	<0.001
Drift	1, 218	5.17	0.024
Pool	1, 218	6.13	0.014
Hyporheic	1, 218	10.25	0.002
<u>Sweltsa Biomass</u>			
Edge	1, 218	200.14	<0.001
Riffle	1, 218	170.56	<0.001
Drift	1, 218	55.78	<0.001
Pool	1, 218	115.57	<0.001
Hyporheic	1, 218	43.42	<0.001
<u>Ameletus Biomass</u>			
Edge	1, 218	2.46	0.118
Riffle	1, 218	1.96	0.163
Drift	1, 218	0.05	0.831
Pool	1, 218	1.28	0.259
Hyporheic	1, 218	0.7	0.403
<u>Baetis Biomass</u>			
Edge	1, 218	24.21	<0.001
Riffle	1, 218	30.29	<0.001
Drift	1, 218	0.02	0.88
Pool	1, 218	0.11	0.738
Hyporheic	1, 218	2.26	0.134
<u>Cinygmula Biomass</u>			
Edge	1, 218	3.95	0.048
Riffle	1, 218	35.61	<0.001
Drift	1, 218	3.65	0.058
Pool	1, 218	1.16	0.283
Hyporheic	1, 218	0.11	0.74
<u>Suwallia Biomass</u>			
Edge	1, 218	20.76	<0.001
Riffle	1, 218	45.71	<0.001
Drift	1, 218	1.81	0.18
Pool	1, 218	15.01	<0.001
Hyporheic	1, 218	8.13	0.005

Discussion

Macroinvertebrate density, biomass, and richness

We found that macroinvertebrates in riffle habitats were the most highly disturbed communities among those evaluated. Macroinvertebrate density, biomass, and richness significantly declined in riffle habitats during the salmon run. Other studies in Alaska streams have documented reductions in riffle macroinvertebrate abundance and richness during salmon spawning (Moore et al. 2004, Lessard and Merritt 2006, Moore and Schindler 2008, Monaghan and Milner 2009). Studies in New Zealand and Michigan streams have also shown that spawning salmon reduce riffle macroinvertebrate richness (Hildebrand 1971, Field-Dodgson 1987). This macroinvertebrate response is likely due to the large number of invertebrate taxa unable to survive the intense bioturbation impacts from salmon during migration and spawning activities in main-channel habitats (see also Janetski et al. 2009).

Several studies have shown that pool refugia habitats retain more macroinvertebrates compared to other habitats during flood disturbance events (Lancaster and Hildrew 1993, Winterbottom et al. 1997, Lancaster 2000). However, in response to salmon disturbance, we found that total insect biomass significantly decreased in backwater pools, and only one taxon, the midge *Chironomus* significantly increased in pools during the salmon run. Perhaps the high historical timber harvest activity of the Twelve Mile Creek watershed (whereby 68% of the total watershed was harvested) diminished the quality of backwater pools. Without appropriate riparian management, logging can alter channel complexity by eliminating large wood retention, reducing overall stream habitat heterogeneity and consequently altering pools and other habitats

(Duncan and Brusven 1985). Over time, reductions in large wood inputs can cause a shift in channel morphology toward wider, shallower channels and finer sediment size due to fine particle erosion from unstable riparian banks (Barr and Swanston 1970, Hawkins 1982). Perhaps the reduced habitat heterogeneity of Twelve Mile Creek provides backwater pools that are not suitable refugia for macroinvertebrates that may have otherwise colonized pools during salmon disturbance activities. Alternatively, changes in the overall stream channel may also reduce the resettlement efficacy of dislodged and passively drifting macroinvertebrates into lower quality pools if the flow conditions are inappropriate. Macroinvertebrate density and taxonomic richness significantly increased in the hyporheic zone during salmon spawning, suggesting the hyporheos is a refuge for certain macroinvertebrates during salmon spawning. Other studies have recognized the hyporheic zone as an important refugium for aquatic macroinvertebrates and other river organisms during hydrological disturbances such as floods and droughts (Williams and Hynes 1974, Oliver et al. 1997, Rosario 2000).

Macroinvertebrate density and richness of drift increased significantly during salmon spawning. A study in Alaska found that total invertebrate drift was 2-4 times greater during sockeye salmon (*Oncorhynchus nerka*) spawning as compared to pre and post drift (Peterson and Foote 2000). Another study in coastal Alaska found that the massive streambed disturbance due to salmon significantly increased macroinvertebrate drift density (Monaghan and Milner 2009). Spawning salmon likely caused catastrophic drift of macroinvertebrates. Alternatively behavioral drift may have been for a component of increased drift if these benthic macroinvertebrates have evolved life history traits to avoid spawning disturbance. The literature on drift propensity shows that

behavioral drift is a crepuscular activity (Waters 1972, Hynes 1975, Chutter 1975, Waters and Hokenstrom 1980). We sampled drift at noon to avoid behavioral drift, and thus, drift in this study should represent primarily those individuals that have been dislodged due to spawning activities.

Insect Order-Level Response to Spawning Salmon

Ephemeroptera and Diptera biomass significantly declined in riffles during salmon spawning. Others studies from Southeast Alaska found significant declines in riffle mayfly taxa during salmon spawning such as *Baetis*, *Seratella* (Ephemeroptera: Ephemerellidae), *Drunella grandis* (Eaton) (Ephemeroptera: Ephemerellidae), *Cinygmula*, and *Drunella doddsi* (Needham) (Ephemeroptera: Ephemerellidae) (Lessard and Merritt 2006, Lessard et al. 2009). The most dominant dipteran family in Twelve Mile Creek was the Chironomidae, comprising 82% of total Diptera. Other studies in Alaskan streams have observed declines in Chironomidae density and biomass in riffle habitats during salmon spawning (Peterson and Foote 2000, Moore et al. 2004, Lessard et al. 2009). Plecoptera and Trichoptera biomass was not significantly affected by spawning salmon in riffles, perhaps because they have been reported to feed on abundant salmon tissues associated with post-spawning activities (Ellis 1970, Walter et al. 2006). Plecoptera biomass increased during the salmon run in riffle habitats, and the most dominant plecopteran was the predaceous *Sweltsa*, which may consume the abundant salmon tissues and salmon eggs (Ellis 1970). Trichoptera biomass significantly increased in riffles, and another study found that *Ecclisomyia conspersa* (Trichoptera: Limnephilidae) fed on salmon tissues and increased in abundance in riffle habitats during spawning due to the increased food availability (Walter et al. 2006).

The efficacy of stream edge habitats as refugia appears to be taxa specific.

Diptera biomass significantly decreased in edge habitats during spawning. Dipterans appear to be the least tolerant of spawning disturbance as they significantly decreased in both riffle and edge habitats and did not increase in any potential refuge habitats during the salmon run. Trichoptera biomass significantly increased in edge habitats during salmon spawning. Caddisfly response is likely species-specific, with some species that migrated to edge habitats to avoid salmon disturbance while others were feeding on the abundant salmon carcasses along stream edges as the salmon run progressed (Walter et al. 2006). Trichoptera biomass significantly increased in the hyporheic zone during salmon spawning. Early instar caddisflies may migrate vertically into the more protected hyporheic zone during spawning to feed on organic particles in less disturbed areas of the substrata. Trichoptera biomass significantly decreased in stream drift during the salmon run. This is likely because most caddisflies appeared to migrate to stream edges during salmon spawning. Plecoptera biomass increased appreciably in stream drift during salmon spawning. Plecopterans are perhaps highly susceptible to bioturbation due to spawning salmon and may be very easily dislodged from the benthic substrates.

Functional-Feeding Group Response to Spawning Salmon

Scrapers, collector-filterers, collector-gatherers, and predators all significantly declined in riffle habitats during salmon spawning. This response is most likely due to their feeding behavior, as scrapers forage on biofilm from the tops of rocks in the active channel where redd construction is prevalent and thus are highly vulnerable to bioturbation impacts (Lamberti 1996, Quinn 2005). However, chlorophyll *a* actually increased in riffles during the salmon run, and yet scraper biomass still significantly

declined, a response likely due to abrasion and dislodgement. Another study in Southeast Alaska found declines in riffle macroinvertebrates despite increases in chlorophyll abundance (Chaloner et al. 2004). Collector-filterers are likely easily disturbed by spawning salmon due to their sensitive filter feeding mouthparts that may be abraded by fine sediments dislodged by spawners, or physical displacement by salmon movement. Collector-gatherers may also be easily disturbed by the dislodged sediments and increased turbidity that occurs during spawning that might fill in benthic interstices where collector-gatherers feed. Predators may be low in abundance in riffles due to little prey availability; or they may be feeding on salmon carcasses in low-disturbance habitats such as main-channel pools or stream edges. Shredders significantly increased in riffles during salmon spawning, a response likely due to the concomitant occurrence of leaf litter fall during the late summer salmon run.

Shredders and collector-filterers significantly declined in backwater pools during spawning. Shredders may be moving from pools into riffle habitats to feed on allochthonous leaf litter inputs within riffles. Shredders and collector-filterers may also be susceptible to anoxic conditions that can occur in pools as the salmon run progresses and salmon carcasses build up and decompose in backwater pools. Collector-filterers increased, though not significantly, in edge habitats during salmon spawning. This is likely due to decreased disturbance from spawners in edge habitats as collector-filterers appeared to decline in riffle habitats and increase in edge habitats during spawning.

The hyporheic zone is an important ecotone between surface and ground water which supports several resident fauna, typically meiofauna less than 1mm, such as water mites, early instars of aquatic insects, rotifers, segmented worms, flatworms, and

crustaceans (Boulton et al. 1998). Shredder, collector-gatherer and collector-filterer biomass significantly increased in the hyporheic zone during spawning. These functional feeding group taxa may migrate vertically into the hyporheic zone during spawning to feed on organic particles in less disturbed areas of the substrata. Also, predator and collector-gatherer biomass increased appreciably, though not significantly, in stream drift during the salmon run. Predators and collector-gatherers are perhaps highly susceptible to bioturbation due to spawning salmon and may be very easily dislodged from the benthic substrates. Collector-filterers decreased in drift during the salmon run and instead may be migrating or be displaced into stream edge and hyporheic habitats as refuge from spawner disturbance.

Specific Taxa Responses to Spawning Salmon

Midges belonging to the genus *Chironomus* significantly decreased in riffles and backwater pools, and significantly increased in the hyporheos and drift during the salmon run. Perhaps these collector-gatherers were disturbed in riffles and pools due to lack of organic matter in benthic interstices that spawners dislodged during spawning activities. *Chironomus* biomass may have also declined in riffles and pools due to the fact that Twelve Mile Creek is a heavily harvested watershed with relatively small sediments that may be readily dislodged by spawners. In contrast to our findings, another study in Southeast Alaska found increases in Chironomidae biomass during salmon spawning and postulated that this may be due to well developed dispersal ability along with fast reproduction and development (Armitage et al. 1995, Chaloner et al. 2004).

The three most dominant mayfly taxa in Twelve Mile Creek were *Ameletus*, *Baetis*, and *Cinygmula*; *Baetis* and *Cinygmula* significantly decreased in riffles during the

salmon run. Others studies from Southeast Alaska found significant declines in riffle mayfly taxa during salmon spawning (Lessard and Merritt 2006, Lessard et al. 2009). Another study in the Pacific Northwest found significant declines of *Baetis* and *Cinygmula* mayflies during salmon redd excavation in riffle habitats (Minakawa and Gara 2003). *Baetis* and *Cinygmula* mayflies significantly decreased in edge habitats during the salmon run. Edge habitats are not a refuge for these two genera and *Baetis* and *Cinygmula* may be especially vulnerable to spawning activities due to their modes of feeding. *Baetis* is a collector-gatherer that feeds on fine particulate organic matter within benthic sediments which may become dislodged during spawning activities, thus reducing *Baetis* food availability. *Cinygmula* is a scraper that scrapes benthic biofilm from the tops of rocks in the main-channel. A study looking at benthic biofilm within Twelve Mile Creek found spawning salmon reduced algal abundance, thus also reducing the major potential food resource for *Cinygmula* (Tiegs et al. 2008).

Sweltsa density increased while *Suwallia* density decreased in riffles, the hyporheos, backwater pools, and stream edges during the salmon run. These results may be due to evolutionary competitive exclusion of these very similar predacious Chloroperlidae stoneflies. Prior to the salmon run, *Suwallia* was the dominant plecopteran in Twelve Mile Creek, and then their abundance dropped to nearly zero in all habitats during the salmon run. *Sweltsa* stoneflies were not present at all in any habitats prior to salmon arrival and then became overwhelmingly dominant in all habitats during the salmon run. It is quite possible that such similar genera have adapted life histories that limit direct competitive interactions and minimal physical overlap with *Sweltsa* being the most abundant predator to feed on salmon tissues during the spawner run (Ellis 1970);

the ghost of competition past (Connell 1980). While *Suwallia* likely feeds on invertebrates prior to salmon arrival and then emerges before the salmon run to avoid competition with *Sweltsa* stoneflies. *Sweltsa* stoneflies significantly increased in stream drift during salmon spawning, a result likely due to their high abundance in all habitats during the salmon run and they may be easily dislodged from benthic substrates.

Conclusions

Disturbance is a central organizing factor in stream ecology (Resh et al. 1988) and is fundamental to the concept of patch-dynamics whereby ecosystems are viewed as both temporally and spatially variable mosaics, in which patchiness is established by the heterogeneous impacts of disturbance (White and Pickett 1985). Spawning salmon create patches of disturbance through redd digging and upstream migration which shifts the colonization and community structure of benthic macroinvertebrates (Milner et al. 2008). We demonstrated that benthic disturbances from spawning salmon altered the distribution, abundance, and community composition of benthic organisms and caused significant reductions of macroinvertebrate communities in riffle habitats where salmon activities are often greatest, a result found in several other studies (Peterson and Foote 2000, Chaloner et al. 2004, Moore et al. 2004, Lessard et al. 2009). However, few studies have investigated the efficacy of macroinvertebrate refugia habitats in response to spawning salmon disturbance.

Studies regarding macroinvertebrate utilization of refugia in response to disturbance have largely focused on flow (Palmer et al. 1991, Lancaster et al. 1993, Negishi et al. 2002, Olsen and Townsend 2005) and the use of refugia in response to

spawning salmon is poorly understood. This research elucidated some of the mechanisms of macroinvertebrate persistence throughout the annual benthic disturbance due to spawning salmon. This research also demonstrated that the observed macroinvertebrate response to disturbance depends on where samples are taken within a stream channel. Most studies that show reductions in macroinvertebrate abundance in response to spawning activity were sampled from riffle habitats (Duncan and Brusven 1985, Minakawa and Gara 2003, Tiegs et al. 2009, Monaghan and Milner 2009). However, if refugia habitats were sampled instead, one might observe increases in macroinvertebrate abundance and richness during spawning disturbance. Biomonitoring and other benthic studies should include sampling from several habitat types in order to get a broader view of how macroinvertebrates are responding to disturbance impacts. This study supports the theory that stream habitat heterogeneity is a vital feature that mediates spawning salmon disturbance impacts (Monaghan and Milner 2009). The function of certain in-stream habitats such as backwater pools, stream edges, and the hyporheic zone are effective refugia for certain macroinvertebrate taxa. Refugia habitats may be a crucial determinant of macroinvertebrate survivability during the massive annual benthic disturbance from spawning salmon in Southeast Alaskan rainforest streams.

Chapter 3. Macroinvertebrate Community Differences in Riffle and Backwater Pool habitats in Response to Spawning Salmon in Southeast Alaskan streams

Methods

This study was conducted between July and September 2007 in four streams: Nossuk Creek, Indian Creek, Maybeso Creek, and Twelve Mile Creek on Prince of Wales Island, Southeast Alaska, USA (Fig 1). Benthic macroinvertebrates were collected semi-quantitatively within a defined 0.315m^2 area with a D-frame kick net from riffle and pool habitats (Fig 13). This was accomplished by placing a 1m long weighted PVC pipe on the benthos and collecting a sample within the 1m length and the 0.315m width of the D-Net (Fig 14). Each riffle sample was collected for 30 seconds by agitating the benthos at a depth of 8-10cm within a randomly chosen area. The pool samples were collected by sweeping the D-Net within a 0.315m^2 randomly chosen area repeatedly for 30 seconds. The samples were rinsed through a 500 μm sieve and then preserved in 70% ethanol for later processing. All insects were identified to genus or species (except the family Chironomidae, which were left at family) and non-insect taxa were identified to order or family. Samples were collected twice before the salmon run (15th June and 12nd July) and twice during the salmon run (17th August and 20th September) from 6 riffles and pools within a 300m reach of each of 4 streams. Two of the streams were from low-harvest watersheds: Indian Creek and Nossuk Creek, and two of the streams were from high-harvest watersheds: Maybeso Creek and Twelve Mile Creek. Several abiotic factors were collected in each habitat within each stream including: water temperature, % dissolved oxygen, conductivity, pH, % canopy cover, water velocity, and water depth.

Fig 13. Sampling backwater pool habitats (A) and riffle habitats (B).

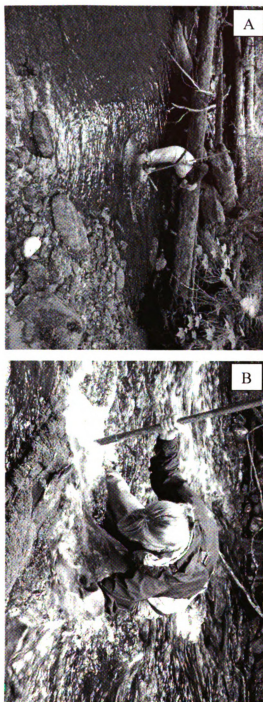


Fig 14. Sampling technique used in riffle and backwater pool habitats in 2007. A 1m long weighted PVC pipe was used to delineate a quantitative area of 0.315m^2 .



Results and Discussion

A non-metric multi-dimensional scaling ordination demonstrated a significant separation of the macroinvertebrate communities in riffle and backwater pool habitats (Fig 15). There was a significant decline in macroinvertebrate abundance in riffle habitats upon salmon arrival within Maybeso Creek (Fig 16), Twelve Mile Creek (Fig 17), and Indian Creek (Fig 18). There was a non-significant decline of macroinvertebrate abundance within riffle habitats during the salmon run in Nossuk Creek (Fig 19). There was no significant change of macroinvertebrate abundance within backwater pool habitats upon the arrival of salmon in any stream. These data suggest that backwater pools may offer refuge for macroinvertebrates during spawning in that pools are stable and protected habitats that sustain macroinvertebrate communities that are not disturbed by spawning salmon. Overall, when the data are pooled, macroinvertebrate abundance declined in riffles and increased in backwater pools (Fig 20). These data also supports the prediction that backwater pools offer refuge to macroinvertebrates during salmon spawning disturbance. Habitat heterogeneity is important as it offers diverse habitat types that sustain diverse and unique taxa (Kerans and Karr 1992, Gjerløv et al 2003). Riffle habitats are often dominated by scrapers, such as heptageniid mayflies, that feed on abundant biofilm and collector-filterers, such as simuliid dipterans, that collect fine particulate organic matter from stream drift. Backwater pools typically sustain shredders, such as limnephilid case-building caddisflies, and collector gatherers, such the Chironomidae (Merritt et al. 2008). Backwater pools represent important reach scale heterogeneity in stream flow and substrate composition, which may offer refugia for macroinvertebrates and other stream organisms (Lancaster 1993).

Figure 15. Non-Metric Multi Dimensional Scaling ordination showing the significant separation of macroinvertebrate community structure in riffle and pool habitats.

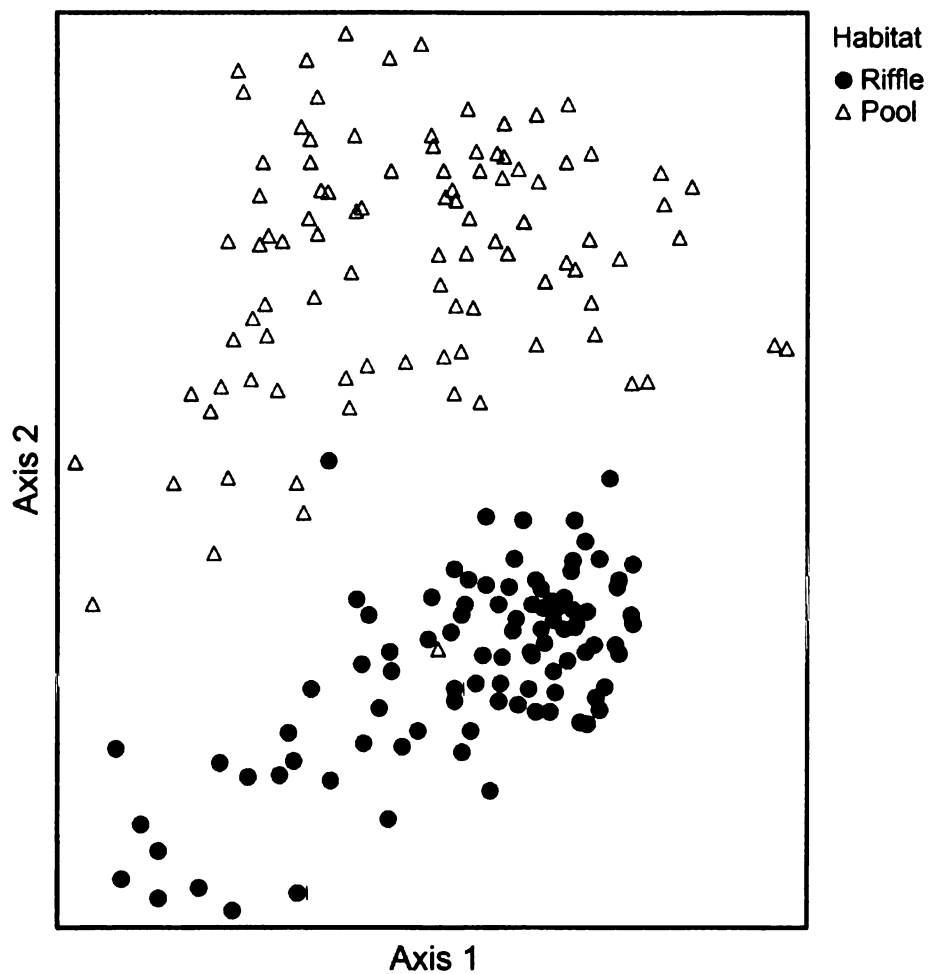


Fig 16. Macroinvertebrate abundance in riffle and pool habitats in Maybeso Creek.

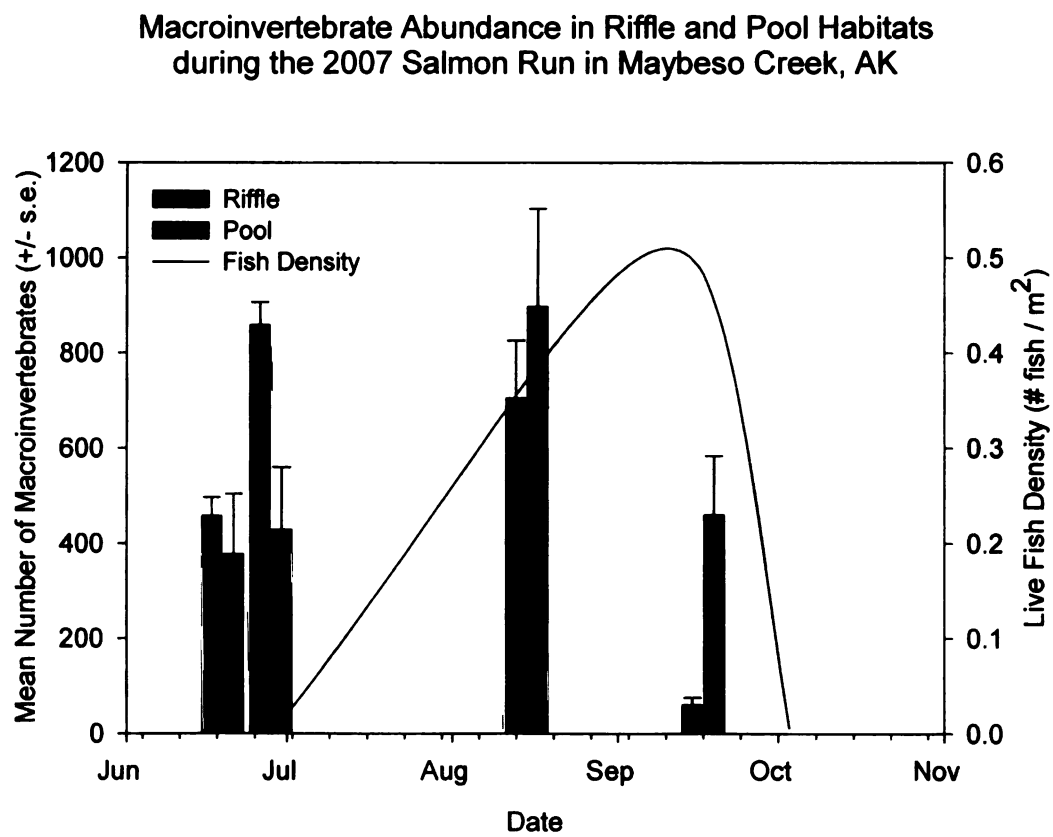


Fig 17. Macroinvertebrate abundance in riffle and pool habitats in Twelve Mile Creek.

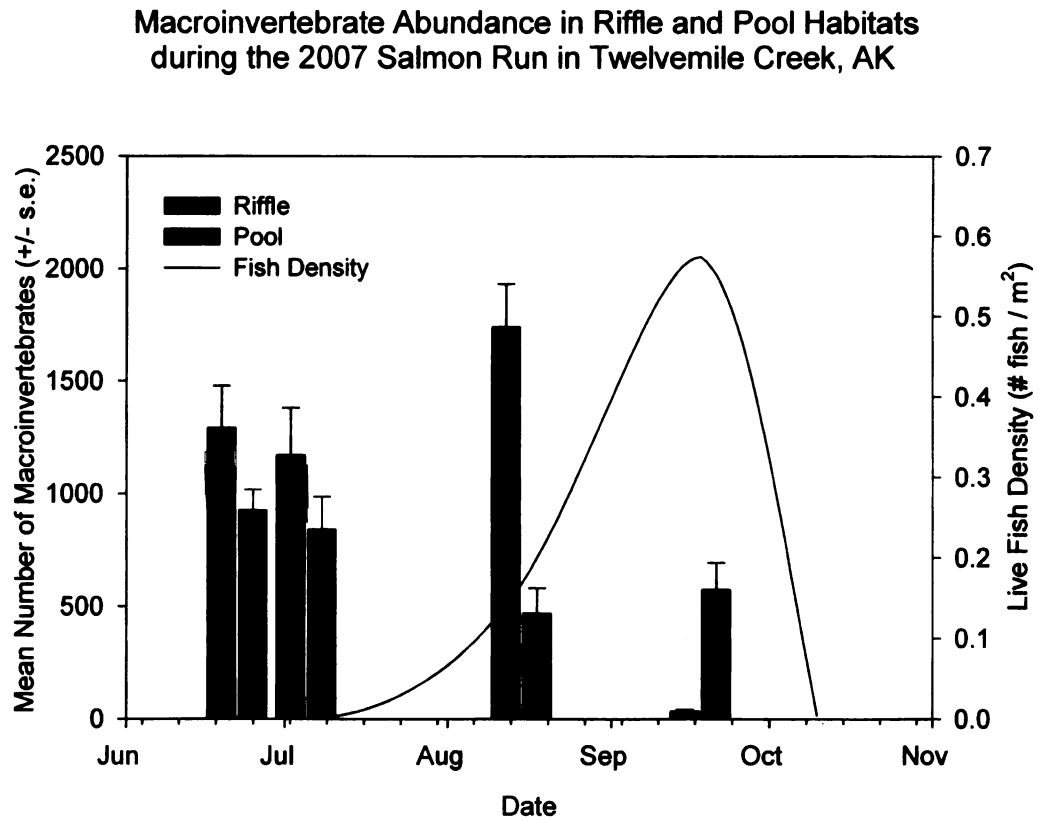


Fig 18. Macroinvertebrate abundance in riffle and pool habitats in Indian Creek.

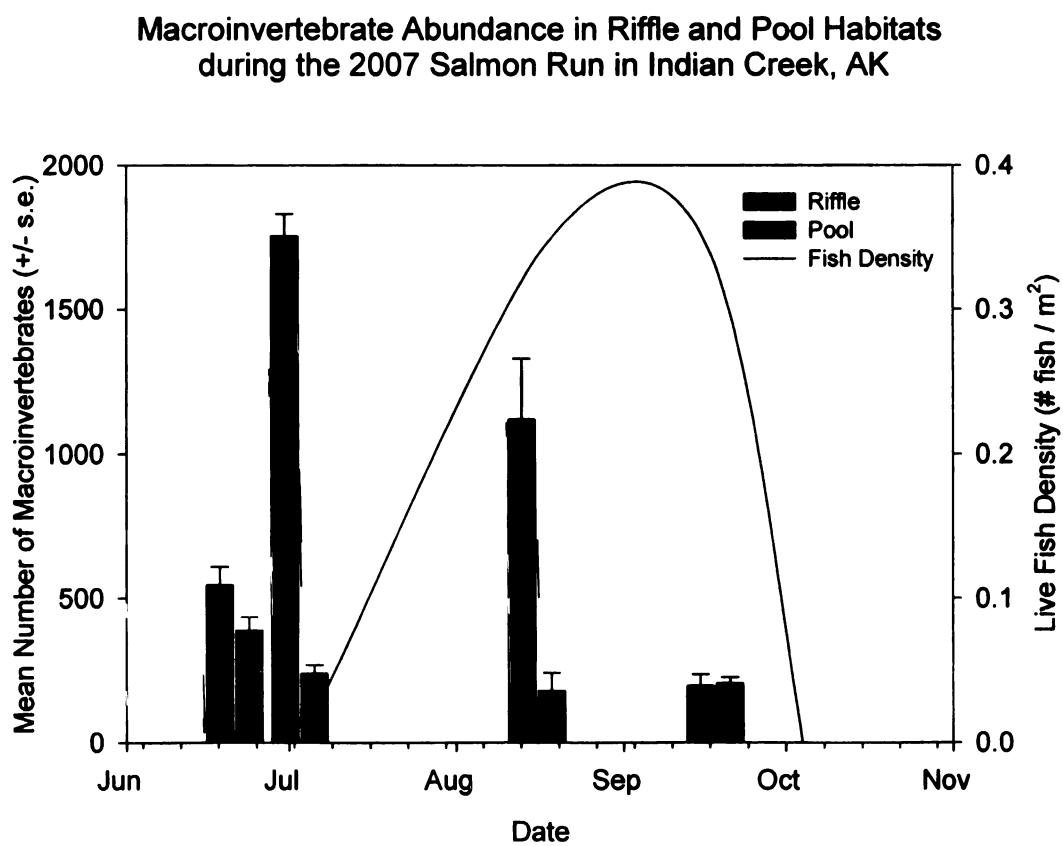


Fig 19. Macroinvertebrate abundance in riffle and pool habitats in Nossuk Creek.

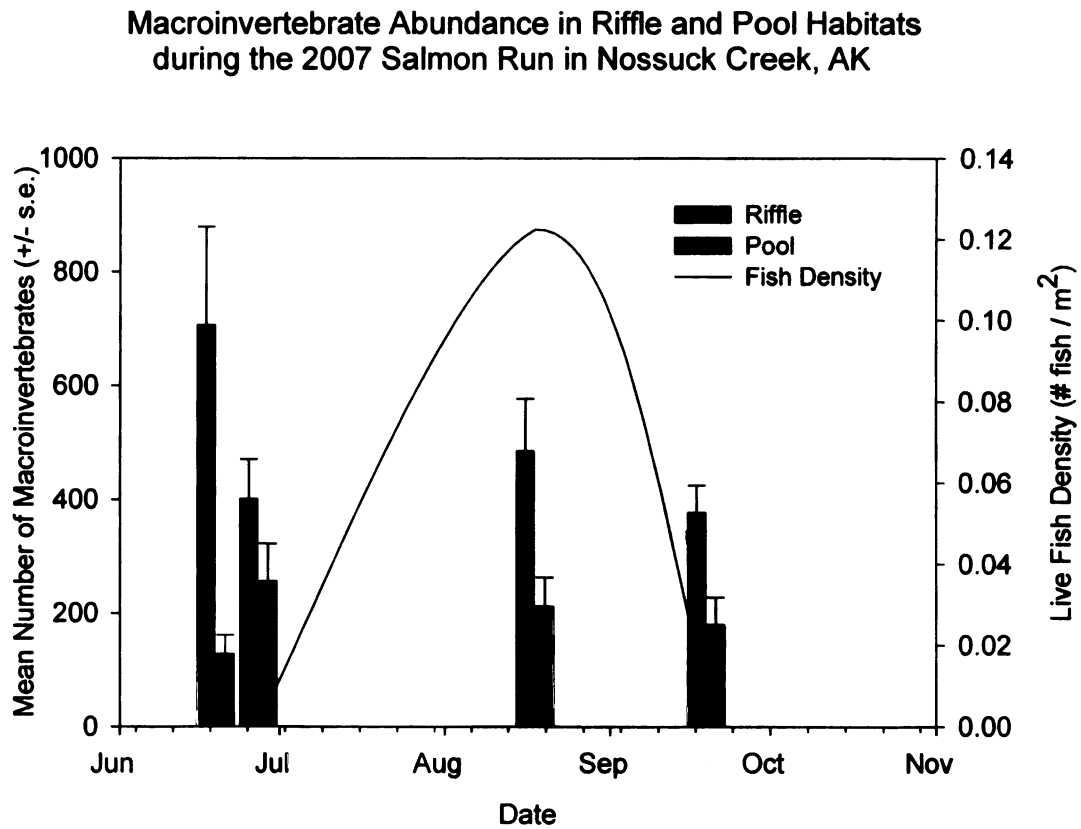
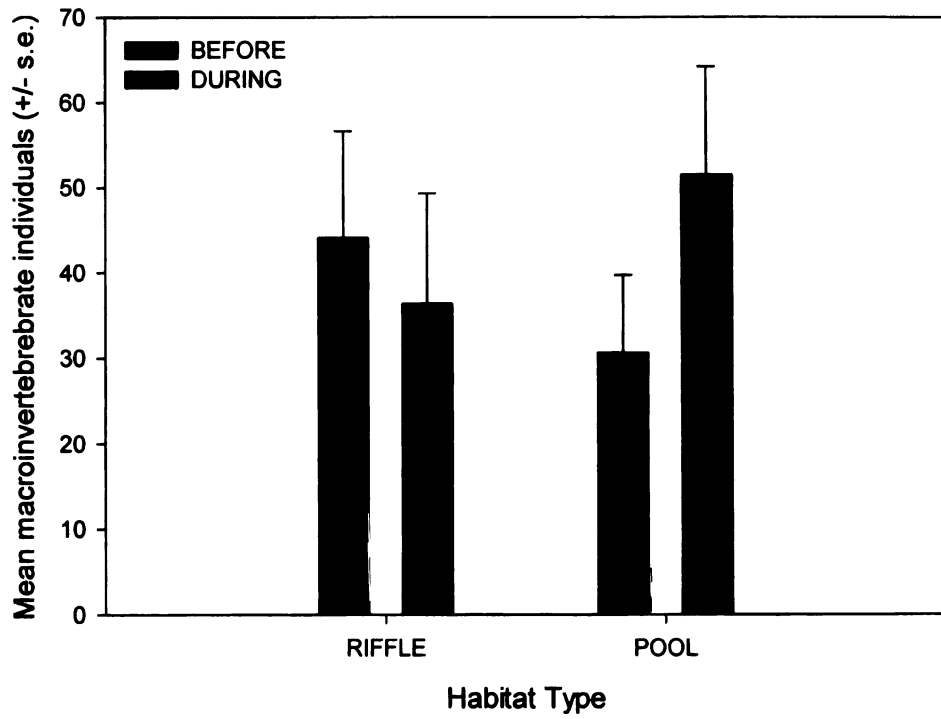


Fig 20. Mean macroinvertebrate abundance in riffle and pool habitats before and during the salmon run.



Appendix 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2010-01

Title of thesis or dissertation (or other research projects):

Macroinvertebrate Community Response to Timber Harvest and Spawning Salmon in
Southeast Alaska Rainforest Streams

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)

Emily Yvonne Campbell

Date May 1, 2010

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America.
Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.

Museum(s) files.

Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix 1.1

Voucher Specimen Data

Page 1 of 5 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:						Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults	Other	
Class: Arachnida, Spider	Twelve Mile Creek, AK Pool 5, 7/15/2008					1		
Class: Arachnida, Sub-Class: Acari	Maybeso Creek, AK Rifle 2(1), 6/28/2007					5		
Class: Hirudinea	Nossuck Creek, AK Pool 5, 8/18/2007					2		
Phylum: Nematomorpha, Hairworm	Maybeso Creek, AK Pool 1, 9/17/2007					2		
Class: Oligochaete, Earthworm	Twelve Mile Creek, AK Edge 3, 7/31/2008					4		
Class: Oligochaete	Indian Creek, AK Pool 1, 7/3/2007					4		
Class: Crustacea, Order: Amphipoda	Maybeso Creek, AK Pool 1, 8/15/2007					1		
Order: Coleoptera, Family: Curculionidae	Nossuck Creek, AK Pool 1, 9/19/2007					1		
Class: Crustacea, SubClass: Copepoda	Maybeso Creek, AK Pool 1, 6/20/2007					2		
Family: Dytiscidae, Genus: <i>Hydrotus</i>	Indian Creek, AK Pool 6, 9/18/2007					1		
Family: Dytiscidae, Genus: <i>Oreodytes</i>	Maybeso Creek, AK Pool 3, 6/20/2007					2		
Family: Dytiscidae, Genus: <i>Oreodytes</i>	Twelve Mile Creek, AK Pool 4, 9/18/2007		1					
Family: Elmidae, Genus: <i>Narpus</i>	Twelve Mile Creek, AK Edge 2, 8/8/2008					1		
Family: Elmidae, Genus: <i>Narpus</i>	Twelve Mile Creek, AK Pool 5, 9/14/2008		2					
Family: Elateridae	Maybeso Creek, AK Pool 3, 6/20/2007		1					
Family: Gyrinidae, Genus: <i>Dineutus</i>	Indian Creek, AK Pool 3, 7/3/2007					1		
Order: Coleoptera, Family: Melyridae	Twelve Mile Creek, AK Hypoheic 5, 8/16/2008					3		
Order: Collembola	Twelve Mile Creek, AK Pool 3, 6/27/2008					2		

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Emily Yvonne Campbell

Date

1-May-10

Voucher No. 2010-01

Received the above listed specimens for deposit in the Michigan State University

Entomology Museum

Curator

5 May 2010

Date

Appendix 1.1

Voucher Specimen Data

Page 2 of 5 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of						Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults	Other	
Order: Coleoptera, Family: Staphylinidae	Twelve Mile, Creek, AK Rifle 3, 8/16/2008		1			1		
Order: Coleoptera, Family: Staphylinidae	Nossuck Creek, AK Pool 5, 6/27/2007					1		
Order: Diptera, Family: Chironomidae	Nossuck Creek, AK Pool 5, 6/27/2007							
Family: Calliphoridae, Genus: <i>Calliphora</i>	Maybeso Creek, AK Pool 2, 9/17/2007		2					
Family: Chironomidae, Filtering-Collectors	Maybeso Creek, AK Rifle 2(1), 6/28/2007		2					
Family: Chironomidae, Gathering-Collectors	Maybeso Creek, AK Rifle 2(1), 6/28/2007		9					
Family: Chironomidae, Predators	Maybeso Creek, AK Pool 2, 6/28/2007		8					
Family: Ceratopogoniidae, Genus: <i>Forcipomyia</i>	Maybeso Creek, AK Pool 2, 9/17/2007		1					
Family: Calliphoridae	Twelve Mile Creek, AK Edge 3, 9/20/2008		1					
Family: Culicidae	Maybeso Creek, AK Rifle 5, 8/15/2007		3					
Family: Ceratopogoniidae, Genus: <i>Probezzia</i>	Indian Creek, AK Pool 1, 7/3/2007		2					
Family: Empididae, Genus: <i>Oreogeton</i>	Twelve Mile Creek, AK Edge 1, 9/20/2008		2					
Family: Psychodidae, Genus: <i>Psychoda</i>	Maybeso Creek, AK Pool 1, 9/17/2007		2					
Family: Simuliidae	Twelve Mile Creek, AK Rifle 2, 9/18/2007		15					
Family: Tipulidae, Genus: <i>Dicranota</i>	Twelve Mile Creek, AK Pool 1, 9/14/2008		2					
Family: Tipulidae, Genus: <i>Hexatoma</i>	Twelve Mile Creek, AK Edge 2, 9/14/2008		2					
Family: Tipulidae, Genus: <i>Ormosia</i>	Twelve Mile Creek, AK Pool 2, 7/23/2008		1					
Family: Tipulidae, Genus: <i>Tipula</i> , Type 1	Twelve Mile Creek, AK Pool 6, 7/5/2007		3					

(Use additional sheets if necessary)

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Curator Date

Appendix 1.1

Voucher Specimen Data

Page 3 of 5 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:						Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults	Other	
Family: Tipulidae, Genus: <i>Tipula</i> , Type 2	Twelve Mile Creek, AK Hyporheic 2, 8/16/2008	1						
Family: Ameletidae, Genus: <i>Ameletus</i>	Nossuck Creek, AK Pool 3, 6/19/2007	4						
Family: Baetidae, Genus: <i>Baetis</i>	Maybeso Creek, AK Rifle 2(1), 6/28/2007	5						
Family: Ephemerellidae, Genus: <i>Drunella</i> , Species: <i>doddsi</i>	Indian Creek, AK Rifle 1, 6/21/2007	2						
Family: Ephemerellidae, Genus: <i>Drunella</i> , Species: <i>flavilinea</i>	Nossuck Creek, AK Rifle 2, 6/19/2007	2						
Family: Ephemerellidae, Genus: <i>Drunella</i> , Species: <i>grandis</i>	Maybeso Creek, AK Rifle 2(1), 6/28/2007	3						
Family: Ephemerellidae, Genus: <i>Serratella</i>	Maybeso Creek, AK Rifle 5, 8/15/2007	7						
Family: Ephemerellidae, unknown	Twelve Mile Creek, AK Edge 3, 7/23/2008	1						
Family: Heptageniidae, Genus: <i>Cinygmula</i>	Maybeso Creek, AK Rifle 2(1), 6/28/2007	10						
Family: Heptageniidae, Genus: <i>Epeorus</i>	Maybeso Creek, AK Rifle 4, 6/19/2007	4						
Family: Heptageniidae, Genus: <i>Rhithrogena</i>	Twelve Mile Creek, AK Edge 3, 9/2/2008	1						
Family: Heptageniidae, unknown	Twelve Mile Creek, AK Edge 3, 8/8/2008	9						
Family: Leptophlebiidae, Genus: <i>Paraleptophlebia</i>	Twelve Mile Creek, AK Hyporheic 1, 7/23/2008	4						
Family: Leptophlebiidae	Twelve Mile Creek, AK Edge 5, 9/20/2008	10						
Family: Aphidae	Twelve Mile Creek, AK Drift B, 9/14/2008					1		
Family: Cicadellidae	Twelve Mile Creek, AK Pool 1, 8/15/2007	1						
Order: Homoptera, Family: Orthetidae	Nossuck Creek, AK Rifle 3, 9/19/2007							
Order: Lepidoptera, Family: Geometridae	Maybeso Creek, AK Pool 4, 9/17/2007	1						

(Use additional sheets if necessary)

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Species or other taxon	Label data for specimens collected or used and deposited	Number of						Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults	Other	
Class: Bivalvia	Maybeso Creek, AK Rifle 5(3), 6/28/2007					1		
Class: Crustacea, Order: Gastropoda	Twelve Mile Creek, AK Drift C, 7/7/2008					1	5	
<i>Oncorhynchus</i> (salmon) egg	Twelve Mile Creek, AK Rifle 3, 9/2/2008							
Class: Ostracoda	Maybeso Creek, AK Rifle 3(1), 6/28/2007					1		
Order: Plecoptera, Family: Capniidae	Twelve Mile Creek, AK Pool 3, 9/2/2008		1					
Family: Capniidae, Genus: <i>Capnura</i>	Twelve Mile Creek, AK Edge 3, 9/20/2008		1					
Family: Chloroperlidae, Genus: <i>Suwallia</i>	Maybeso Creek, AK Rifle 2(2), 6/28/2007		5					
Family: Chloroperlidae, Genus: <i>Sweltsa</i>	Twelve Mile Creek, AK Drift B, 9/20/2008		3					
Family: Chloroperlidae	Maybeso Creek, AK Rifle 5, 8/15/2007		4					
Family: Leuctridae, Genus: <i>Pomoleuctra</i>	Nossuck Creek, AK Rifle 6, 7/6/2007		3					
Family: Nemouridae, Genus: <i>Zapada</i>	Maybeso Creek, AK Rifle 1, 8/15/2007		2					
Family: Perlodidae, Genus: <i>Megarcys</i>	Maybeso Creek, AK Rifle 4, 8/15/2007		2			15		
Phylum: Platyhelminthes, SubOrder: Planania	Twelve Mile Creek, AK Rifle 1, 7/15/2008							
Order: Psocoptera	Twelve Mile Creek, AK Drift A, 8/23/2008					1		
Family: Apataniidae, Genus: <i>Apatania</i>	Twelve Mile Creek, AK Rifle 1, 8/15/2007		7					
Family: Brachycentridae, Genus: <i>Micrasema</i>	Maybeso Creek, AK Pool 4, 8/15/2007		2					
Family: Hydroptilidae, Genus: <i>Stactobiella</i>	Indian Creek, AK Rifle 1, 6/21/2007		2					
Family: Limnephilidae, Genus: <i>Dicosmoecus</i>	Maybeso Creek, AK Pool 1, 6/20/2007		2					

(Use additional sheets if necessary)

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Species or other taxon	Label data for specimens collected or used and deposited	Number of:						Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults	Other	
Family: Limnephilidae, Genus: <i>Ecclisomyia</i>	Maybeso Creek, AK Pool 3, 9/17/2007	3						
Family: Lepidostomatidae, Genus: <i>Lepidostoma</i>	Nossuck Creek, AK Pool 5, 6/27/2007	3						
Family: Lepidostomatidae, Genus: <i>Lepidostoma</i>	Maybeso Creek, AK Rifle 2(3), 6/28/2007		2		1			
Family: Limnephilidae, Genus: <i>Onocosmoecus</i>	Maybeso Creek, AK Pool 5, 6/20/2007		2					
Family: Limnephilidae, Genus: <i>Psychoglypha</i>	Maybeso Creek, AK Pool 2, 8/15/2007		1					
Family: Polycentropidae, Genus: <i>Polycentropus</i>	Maybeso Creek, AK Hyporheic 5, 7/14/2008		3					
Family: Rhyacophiliidae, Genus: <i>Rhyacophila</i>	Nossuck Creek, AK Pool 5, 6/19/2007							
Order: Thysanoptera, Family: Thripidae	Twelve Mile Creek, AK Hyporheic 3, 8/16/2008					3		

(Use additional sheets if necessary)

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