Aquatic Insect Emergence from Headwater Streams Flowing through Regeneration and Mature Forests in Western Oregon

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ABSTRACT

We examined the effect of canopy cover on adult aquatic insect emergence by collecting bi-weekly samples from twelve headwater stream reaches flowing either under a mature conifer canopy or streams flowing through ten-year-old regeneration in western Oregon from February to November 1997. Density and biomass generally followed a bimodal curve with peaks during early spring and summer. Richness was unimodally distributed across time, peaking during mid-season, when abundance began to decline. However, there was a trend showing that headwater streams flowing through young forest supported 1.5-fold-higher insect density and biomass than streams flowing through mature forest (response confined primarily to Diptera). Many families of Diptera were indicators of open-canopy, whereas very few Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera were indicators of either open or closed canopy. The proportional guild and ordinal composition of both density and biomass of the EPT guilds showed few differences between streams flowing through mature and regenerating forests.

INTRODUCTION

Forest management practices impact both terrestrial-riparian and in-stream habitats, water quality, and biota (Blackie et a1. 1980, Campbell and Doeg 1989). Logging and other land use activities are frequently associated with increased stream sediment load, changes to stream channel and hydrology, and altered in-stream faunal populations and communities (Lenat et a!. 1981, Murphy et a1. 1981, Davies and Nelson 1994, Angradi 1999, Kreutzweiser and Capell 2001, Kreutzweiser et a1.2005, Moldenke and Ver Linden 2007). However, the effects of timber harvest on the richness and diversity of macroinvertebrate taxa are not obvious and in some cases oflittle significance (Noel et a1. 1986) but dependent on the width of the remaining riparian buffer (Rykken et a1.2007). Timber harvest in upland forests changes the composition and structure of the riparian plant community (McClellan et al. 2000). Removal of riparian overstory decreases stream shading (Minshall 1978) and increases the amount of solar radiation reaching the stream bottom, thus causing an increase in water temperature (Cummins and Klug 1979, Wilkerson et al. 2006) and potentially shifting the primary source of food from allochthonous to autochthonous. This change is a fundamental factor affecting in-stream macro invertebrate communities (Stockner and Shortreed 1976, Hawkins et al, 1982, Duncan and Brusven 1985). Earlier studies have shown that both insect and periphyton production are higher in stream reaches with open canopy than in those with closed canopies (Gregory 1980, Newbold et a1.1980, Murphy and Hall 1981, Hawkins et al. 1982). We undertook a study -in Oregon to document the effect of canopy removal on the flying insect resource produced by headwater streams.

In the Pacific Northwest, removal of the climax conifer canopy cover potentially initiates a process of succession in the stream insect community. Stream inputs are shifted

from coniferous to deciduous litter that contains nutrients that are more mobile in the ecosystem (Cummins and Klug 1979). Murphy et al. (1981) found higher rates of microbial respiration and greater biomass of aufwuchs, benthos, drift, salamanders and trout in streams traversing open canopy stands than streams flowing through an enclosed canopy forest. Meehan (1996) noted that the abundance of aquatic insects was higher in non-canopied streams than forested streams in Oregon and that the difference was reflected in a consequent change in the diet of fish.

Our hypothesis was that unshaded streams would provide a higher density and biomass of emerging aquatic insects than shaded streams. Ifhigher densities did occur, then wc predicted a correlative shift in feeding guild composition caused by altered resources between streams flowing through early regeneration and mature forest (i.e., increased shredder adults in the late fall and early spring and increased collector adults throughout the entire growing season). An associated goal was to document whether significant loss of any forest-dependent taxa would be present 10-years following harvest.

METHODS AND MATERIALS

We placed an emergence trap in each of four headwater stream reaches on each of three watersheds in westem Oregon forests dominated by Douglas-fir *(Pseudotsugam menziesii* and western hemlock *(Tsuga heterophylla).* These low-gradient streams flowed through early successional (approx. 40 acre; < 10 years old) (two at each site) and mature forested (50-150 years old) (two at each site) uplands. Both a permanent and a temporary stream were sampled at each stage of succession at each site (Progar and Moldenke 2002). These watersheds were: Lookout Point (45°28'45"N, 122° 8'8"E), 675 m elevation; Keel Mountain (44°3l'4l"N, l22°37'55"E), 700 m elevation; and Sand Creek (44°46'8"N, 123°35'40" E), 374 m elevation. **In** the clearcut areas, timber was removed to the stream edge. The riparian vegetation bordering these first order streams was comprised of narrow riparian strips of alders *(Alnus* spp.) at Keel Mountain, diverse woody shrubs and trees at Lookout Point, and willows *(Salix* spp.) at Sand Creek. At ten years post-harvest, all streams had developed a shrub cover that provided herbaceous stream inputs. The alders and willows in the regenerating stands had multiple levels of dense canopy that produced copious litter, but the alders in the mature forest were tall and spindly and produced limited deciduous litter.

Adult aquatic insects were sampled with a 1 m^3 emergence trap in each stream in each watershed as has been described previously (Progar and Moldenlce 2002). The traps were operated continuously from mid-February to early November 1997, and the contents were emptied twice a month. Members of Ephemeroptera, Plecoptera, and Trichoptera were identified to genus, and those of Diptera were identified to family. Representative samples were archived in the insect collection of Oregon State University. Biomass was determined by taking the average wet-weight (nearest mg) of 5-10 members of each taxon (not corrected for weight loss due to storage in glycol). Biomass samples were taken at random from the entire study period. Most of the taxa were assigned to functional groups (Menitt and Cummins 1996). Dipterans that could not be assigned to a functional feeding group because family level identification was too coarse to permit functional assignment (e.g., Ceratopogonidae, Chironomidae, Ephydridae, and Tipulidae) were omitted from the analysis of functional feeding guilds but not from the analyses by order and total emergence. Dipterans associated with terrestrial soil habitats were also omitted from analysis.

Analysis of variance (ANOVA; SAS 1989) was used to test for differences in density and biomass (Sokal and Rohlf 1981). Some taxa and functional feeding groups met the assumptions of normality. However, collector, predator, scraper, shredder, Ephemeroptera, Plecoptera, and Trichoptera biomasses and densities were log transformed, and Dipteran densities were square root transformed. The data were pooled for analysis by

season, which was defined by a natural change in the abundance, biomass and composition of the emergent population (Fig. 1) - spring (April 4 - Jun. 26) and summer (Jun. 27 - Sept. 29). Fall and winter catches were excluded from seasonal analyses because of limited numbers. Traps could not be maintained through mid-winter due to road closure by snowfall and rapid discharge events that affected trap integrity.

We used indicator species analysis (PC-ORD, McCune and Mefford 1999) to determine significant indicator taxa for the sampling period for forested and regeneration headwater streams (Dufrene and Legendre 1997). This method calculates a taxon's importance in *a priori* groups of sample units, defined by environmental or habitat differences of interest. It combines, by multiplication, the abundance of a taxon in a specified group relative to its abundance in all groups with that taxon's frequency of occurrence in the sample units in the specified group. The resulting value, expressed as a percentage of perfect indication, describes a taxon's reliability for indicating a grouping parameter such as canopy cover. Statistical significance was based on the proportion of 1,000 randomized regrouping trials that equaled or exceeded the maximum indicator value observed (Monte Carlo test); $a < 0.10$.

To address the question of the relationship between canopy cover (clearcut or mature forest), and season (spring or summer), and their interactions on emergent insect

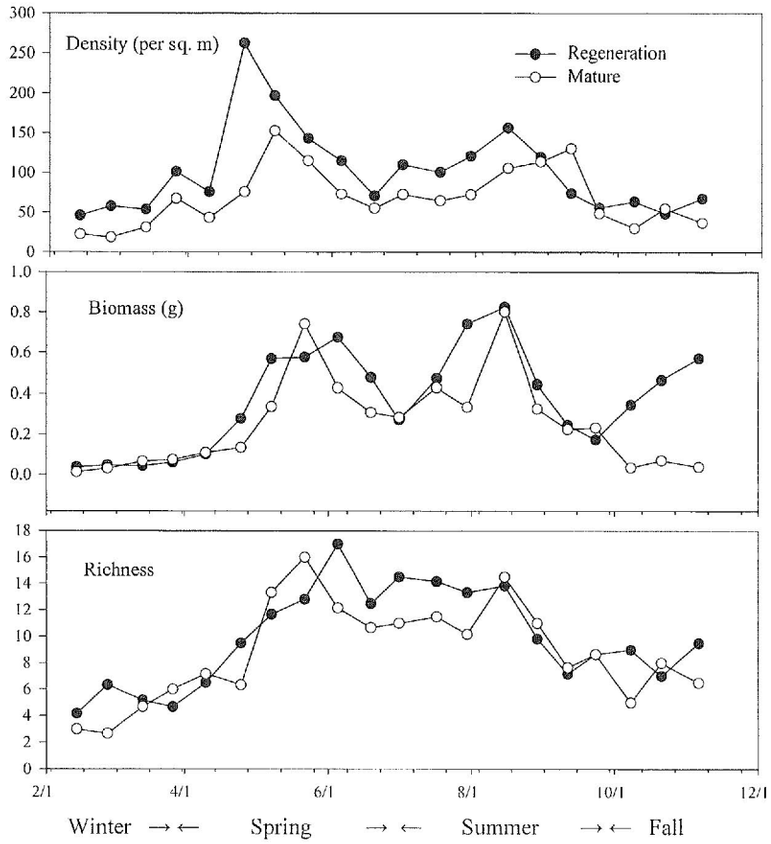

Figure 1. Density (individuals/m^2), biomass (g/m^2), and richness of aquatic adult insects collected from headwater streams flowing through regeneration and mature forested uplands (points are the average of three sites).

abundance and biomass, the following statistical model was fit to the data:

$$Yijkl = /l + \sim j + \sim + \backslash/Iij + Vk + (XV)jk + Aijk SI + (XS)jl + (VShl + (XVS)jkl + Eijkl$$

where Yijkl is the overall sum of biomass/abundance of insects for the 11hseason for the kth stream flow type with the jth canopy cover in the ith watershed,

~l is the overall mean ofY,

B, is the random effect of watershed i, that adds variability to the value ofY, **i** = 1,2,3,

Xi is the fixed effect of the jth level of forest cover type, j= 1,2,

\/Iij is the random effect offorest type that adds variability to Y,

Vk is the fixed effect of the kth forest type, k= 1,2,

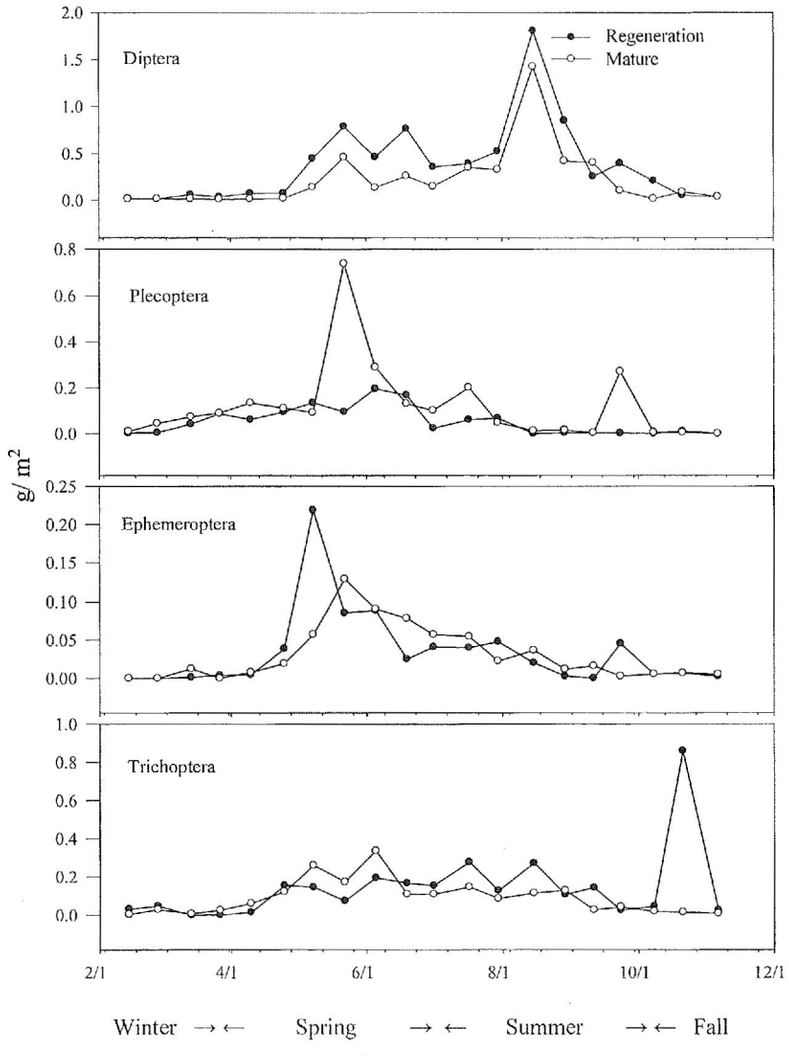

Figure 2. Average biomass (g per m^2 of stream bed) of Diptera, Plecoptera, Ephemeroptera, and Trichoptera from headwater streams flowing through regeneration and mature forested uplands.

XV_{jk} is the fixed effect of the interaction between forest cover type and stream flow type,

^ijk is the random effect of the stream flow type that adds variability to Y,

S^1 is the fixed effect of the lth level of season, 1=1,2,

XS_{jl} is the fixed effect of the interaction between forest type and season,

VS_{kl} is the fixed effect of the interaction between stream flow type and season,

XVS_{jkl} is the fixed effect of the interaction between forest type, stream flow type and season, and

Eijkl is the random effect of seasonthat adds variability to the value of Y.

B_j , Yij ,Eijkl , and ^iji< are all independent with distributions ~N(O,$_o^2$).

This model was fit to the data using PROC MIXED in SAS 9.1. A RANDOM statement was written to ensure that the random effects of the split-split treatment arrangement were accounted for (split on stream type and season). LSMEANS statements were used to generate treatment means, SE's, and 95% confidence intervals. ESTIMATE statements were used to estimate differences between treatments and the SE's and 95% confidence intervals for the differences. Confidence intervals were adjusted for multiple comparisons using the Dunnett method. Residuals were assessed for fit with model assumptions using the PROC UNIV ARIATE procedure. The effect of stream flow type (temporary or perennial) was addressed in Progar and Moldenke (2002).

RESULTS

Seasonal density and biomass by taxonomic group

The pattern of insect emergence was bimodal with peaks during May (35-125 individuals/m^2week) and August (35-65/m^2wk, Fig. 1). Separate spring and summer peaks occurred in all three of the watersheds sampled; these two seasons accounted for 84% of the total biomass sampled. An additional fall peak in biomass occurred at Lookout Point and Keel Mountain. There appeared to be strong seasonal differences in the abundance of the orders and feeding guilds (Figs. 2 and 3). Total densities of all the orders were comparable between seasons; however, total biomasses were greater in summer (Table 1). The emergent densities of PIecopter a ($p = 0.01$) and Ephemeroptera were greater during the spring, but more Trichoptera ($p = 0.04$) emerged during summer. The biomasses of both P1ecoptera ($p = 0.002$) and Ephemeroptera were greater during the spring. There was twice ($p = 0.009$) the biomass of Diptera emerging during the summer.

The total density of emerging insects was nearly one and a half times greater from streams flowing through regeneration than from mature forest; biomass was also one and a half times greater from streams flowing through regeneration (Table 2). Densities of Diptera and Trichoptera were greater from streams flowing through regeneration. The biomasses of Diptera and Trichoptera were greater in the regeneration also. Plecoptera biomass was greater emerging from mature forest.

Functional feeding guilds

The emergence densities and biomasses of scrapers, predators, and collectors were greater from streams flowing through regeneration (Table 2). Shredder biomass was greater from streams flowing through mature forest. The densities of scrapers and shredders ($p = 0.04$) were greater during spring, and those of predators ($p = 0.02$) were greater during the summer. Likewise, the seasonal biomasses of shredders ($p=0.007$) and scrapers were greater in the spring.

Shredders and collectors had the highest proportionate density regardless of cover type during the spring, whereas predators and collectors had the greatest density and biomass during the summer. Shredders comprised 27% of the emergence biomass from streams flowing through mature forest, but only 12% in regeneration; scrapers comprised

5% in regeneration, but 2% in mature forest; while predators comprised a comparable 35% of the emerging biomass from streams flowing through mature forest and 33% in regeneration. Collectors comprised 51% of the emergence biomass from streams flowing through regeneration and 36% of the biomass from streams flowing through mature forest.

Diversity and indicator taxa

Indicator analysis showed that eleven taxa were significantly associated with either streams flowing through mature forest or under a regenerating forest canopy (Table 3).

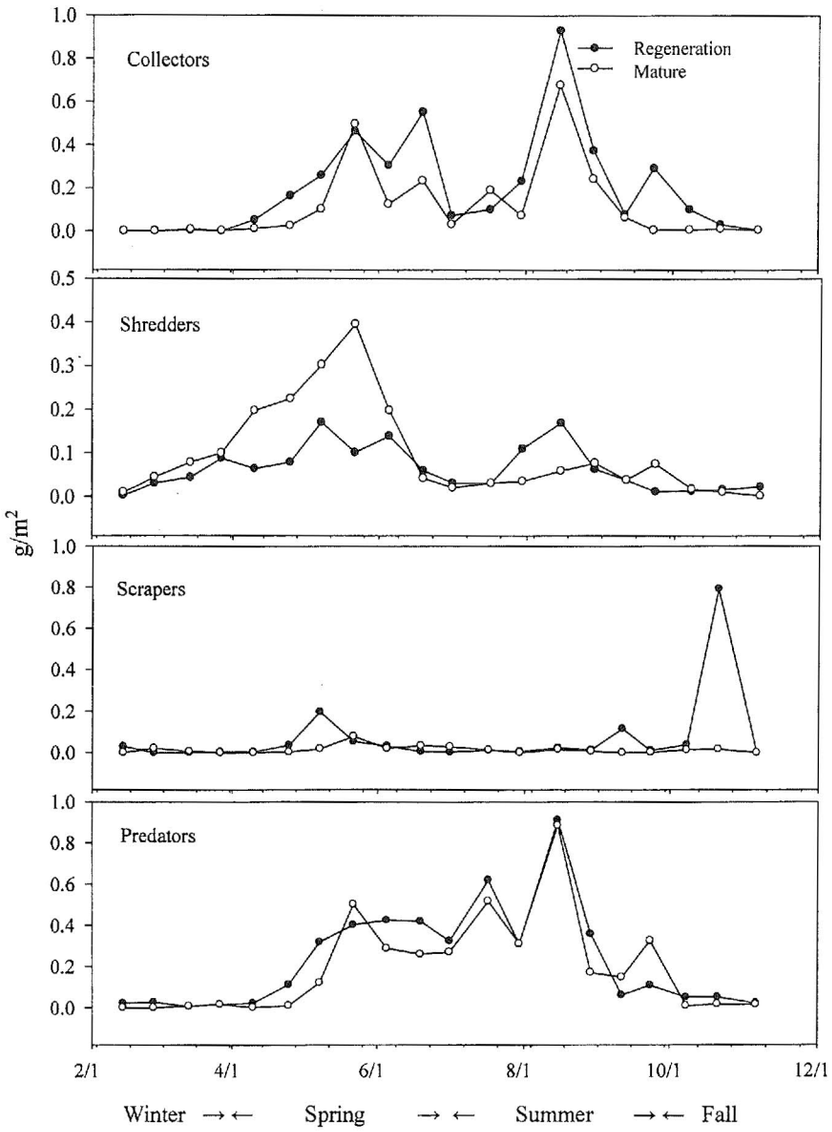

Figure 3. Average biomass (g per square meter of stream bed) of collectors, shredders, scrapers, and predators from headwater streams flowing through regeneration and mature forested uplands.

Two genera of Plecopter a and one genus of Trichoptera were associated with streams flowing under a mature forest canopy. There were two genera of Trichoptera, one genus of Ephemeroptera, and five families of Diptera significantly associated with streams flowing under the canopy of a regenerating forest. Regression of richness on abundance for each of the four streams flowing through the three watersheds indicated that there was no consistent effect of canopy on the richness of the adult aquatic insects emerging from headwater streams ten years after tree harvest.

The temporal emergence patterns of the 13 most abundant EPT genera fell into three groups (Fig. 4): a) genera with similar densities between canopy types that emerged earlier from streams flowing through regeneration than from mature forest (e.g., *Sweltsa, Zapadaa;* b) genera that emerged earlier and had higher density from streams flowing under a mature forest canopy, (e.g., *Moselia, Paraleptophlebia);* and c) genera that were more abundant and emerged earlier from streams flowing through regenerating stands than from streams flowing under a mature forest canopy (e.g., *Cinygma, Wormaldia, Dolophilodes, Lepidostoma, Discosmoecus).*

DISCUSSION

Overall density and biomass

There are few published estimates of the biomass of adult aquatic invertebrates produced from streams in the Pacific Northwest. However, Hawkins et al. (1982) reported that in pool environments the biomass of each of the aquatic orders was similar between

Table 1. Average biomass (g) and density (in parentheses; ind./m^2) in spring and summer averaged over three sites and four streams and ANOVA of order and functional feeding groups of adult aquatic insects collected from emergence traps in headwater streams flowing through 10-year-old regeneration and mature forests. Chironomidae and a few minor Diptera were included in order analyses but excluded from analysis of functional feeding guilds.

Group	Spring	Summer	F value	P value
Ephemeroptera	0.21 (53)	0.10 (25)	2.78 (0.62)	0.13 (0.45)
Plecoptera	056 (114)	0.20 (12)	20.15 (19.18)	0.002 (0.01)
Trichoptera	0.46 (22	0.43 (47)	0.41 (7.98)	0.53 (0.04)
Diptera	0.91 (480)	1.91 (574)	1.53 (11.79)	0.25 (0.009)
Sum of all orders	2.14 (670)	2.64 (659)	1.28 (1.82)	0.29 (0.21)
Collectors	0.73 (66)	0.71 (70)	1.34 (0.10)	0.28 (0.77)
Shredders	0.54 (114)	0.14 (29)	12.73 (5.54)	0.007 (0.04)
Scrapers	0.09 (25)	0.02 (7)	2.41 (0.00)	0.20 (0.96)
Predators	0.47 (20)	0.60 (57)	1.80 (8.49)	0.22 (0.02)

old-growth and clearcut forest types. Anderson (1992) also provided similar biomass estimates for three stages of forest succession from 3rd order streams for all emerging aquatic invertebrates - 1.65 g dry weight/m^2 yr from clearcut forest, 1.53 g dry weight/m^2yr from 40-year-old deciduous regeneration, and 1.65 g dry weight/$m_2$yr from old-growth forest; though Diptera comprised only about 30% of the total biomass, it comprised 77.2% of the total density.

We found total biomass of 4.60 g wet weight/m^2 sampling period in mature forest and 6.04 g wet weight/rrr' sampling period in early regeneration forest - only a 1.3-fold difference. Like Anderson (1992), the majority of our captures was Diptera (density = 79.6%), with EPTs comprising only 43.9% hy weight. The period of peak emergence from these headwater streams was from May 1 to August 15 (with a distinct diminution during late June through early July).

Taxonomic categories

The abundance ofDiptera emerging from headwater streams flowing through early successional regeneration in the spring was nearly twice that of mature forest. Murphy and Hall (1981) and Banks et al. (2007) noted that biomass, density, and richness of EPTs were

Table 2. Average biomass (g) and density (in parentheses; ind./m^2) for the entire study period summed across date and averaged over three sites and two streams for streams flowing through young regeneration forest and streams flowing through mature forest and ANOVA of order and functional feeding groups of adult aquatic insects collected from emergence traps in headwater streams flowing through 10-year-old regeneration and mature forests. Chironomidae and a few minor Diptera were included in order analyses but excluded from analysis of functional feeding guilds. Plecoptera, Trichoptera, and scrapers were pooled across stream flows due to instability of the variance in the spil-plot ANOVA.

Group	Regeneration	Mature	F value	P value
Ephemeroptera	0.34 (87)	0.31 (77)	0.97 (10.67)	0.42 (0.08)
Plecoptera	0.53 (168)	1.18 (170)	0.65 (1.38)	0.50 (0.36)
Trichoptera	1.41 (110)	0.91 (54)	0.08 (2.73)	0.79 (0.24)
Diptera	3.77 (1,565)	2.20 (1,028)	1.54 (3.89)	0.34 (0.18)
Sum of all orders	6.04 (1,929)	4.60 (1,328)	0.02 (1.02)	0.90 (0.42)
Collectors	0.86 (188)	0.57 (123)	1.47 (1.74)	0.34 (0.32)
Shredders	0.20 (199)	0.47 (183)	1.95 (0.24)	0.29 (0.67)
Scrapers	0.08 (49)	0.03 (17)	0.97 (4.76)	0.43 (0.16)
Predators	0.53 (95)	0.54 (59)	0.98 2.68)	0.42 (0.24)

generally higher in low-order streams flowing through clearcuts than in streams of similar size flowing through old-growth forests in Oregon. Nislow and Lowe (2006) found the same trend in New Hampshire. To account for the greater biomass of emerging insects from streams flowing through regenerating stands, we assume that either a) labile nutrient availability is higher due to increased deciduous litter inputs, b) higher levels of insolation directly augment periphyton production, or c) both, thus causing an increase in the total diversity and quantity of food (Stockner and Shortreed 1976, Herlihy et al. 2005). A11 three ofthese possibilities are supported by the available literature. Our experimental design was not able to distinguish between the competing hypotheses (Murphy and Hall 1981, Murphy et a1. 1981, Dudgeon 1988, Meehan 1996).

Feeding guilds

Hawkins and Sedell (1981) and Hawkins et al. (1982) have analyzed guild structure by stream order and gradient in the Pacific Northwest, All guilds of aquatic invertebrates showed strong correlation with food availability or were indirectly correlated to levels of insolation. In their version of the river continuum model: (a) all of the grazing guilds would be expected to increase in response to canopy removal because of increased sunlight; (b) shredders would increase because the nutrients in the deciduous riparian vegetation of early regeneration are far more labile than nutrients in conifer leaves and bark; and, (c) insect predators would increase correlatively with the increased prey base (Sedell et al. 1975, Haggerty et al. 2002, Heino et al, 2005, Goodman et a1.2006); and (d) running counter to this trend of increasing biomass in open-canopy habitats, resources utilized by scrapers would hypothetically become overgrown with photosynthetic algae and diminish. We also found that shredders decreased in both abundance and biomass with canopy removal. Correlatively, Nislow and Lowe (2006) showed a similar decrease in shredder abundance following canopy removal in New Hampshire.

Like Banks et al. (2007), we found little variation in functional guild composition in headwater streams flowing through mature versus regenerating forests; however, there was significant seasonal variation among some guilds. Collectors and shredders showed two peaks in emergence, one in spring and one in late summer. Predators gradually increased

Table 3. Aquatic insects associated ($p < 0.10$) with 10-year-old regeneration or mature forested headwater streams through Dufrene and LeGendre indictor species analysis. (-) = not present, (+) = present, (i) = significant indicator.

Taxon	Regeneration	Mature forest	P*
Plecoptera			
Megaleuctra sp.	-	i	0.088
Zapada sp.	+	i	0.021
Trichoptera			
Rhyacophila sp.	i	+	0.010
Limnephilus sp.	-	i	0.001
Glossosoma sp.	i	-	0.005
Ephemeroptera			
Ironodes sp.	i	-	0.087
Diptera			
Dixidae	i	-	0.0001
Dolichopodidae	i	+	0.049
Psychodidae	i	+	0.018
Sciomyzidae	i	+	0.051
Simulidae	i	+	0.055

through the spring and peaked in mid-summer. Scrapers were most abundant in the fall (especially in regenerating stands). Hawkins and Sedell (1981) also noted changes among functional feeding guilds through the seasons. They found that guild structure was highly variable among streams but found shredders consistently more abundant in the fall, presumably in response to litter input.

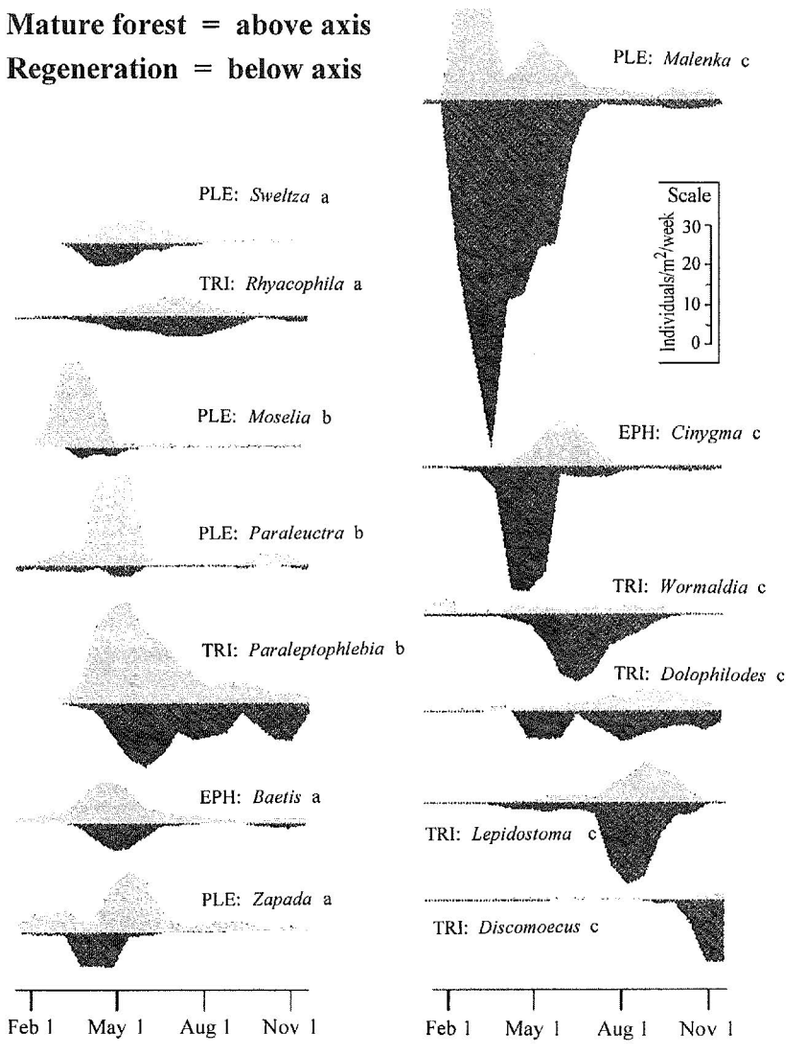

Figure 4. Temporal emergence patterns of the most common EPT taxa from mature forest (above axis) and regeneration (below axis) streams. (a) Those taxa equally abundant from regeneration and streams flowing through mature forest emerged earlier from streams flowing through regeneration than from forested streams (e.g., *Sweltza*, *Zapada*). (b) Taxa more abundant under forest canopy emerged earlier from streams flowing through mature forest than from streams flowing through regeneration (e.g., *Moselia*, *Paraleptophlebia*). (c) Genera associated with regeneration emerge earlier from streams flowing through regeneration (e.g., *Cinygma*, *Wormaldia*, *Dolophilodes*, *Lepidostoma*).

Individual taxa, richness and indicator species

Temperature and photoperiod are among the most important abiotic factors affecting invertebrate life-history. Streamside canopy removal has been shown to increase the water temperature of small streams by 2-5°C (Burton and Likens 1973, Sweeny et al. 1986, Sweeny 1993, Sponseller et al. 2001, Wilkerson et al. 2006). Small shifts in stream temperature (e.g., 1-3°C) have been shown to cause significant changes in growth rate, adult size, and the onset of adult insect emergence (Langford 1975, Sweeny et al. 1986, Rempel and Carter 1987, Baker and Feltmate 1989, Hogg and Williams 1996). As noted in other aquatic invertebrate studies in the Pacific Northwest (Harper et a1. 1995, Anderson et al. 1984, Anderson 1992), the emergence of individual taxa usually occurs within a narrow period of time. Although there is considerable overlap between the peaks of activity of individual species, a stepwise progression of emergence of the most abundant individual EPT taxa occurs through the year. There is a clear progression from stoneflies to mayflies to caddis flies from streams flowing through both mature and regenerating forest covers. Emergence of species primarily found under either an open or a closed canopy was delayed under the less-preferred canopy situation. Among taxa that were equally abundant under both canopy types, emergence occurred earlier under the open canopy conditions. There was a shift in the peak of total activity to two weeks earlier in the regenerating forest. Therefore, the net effect of partial canopy removal within a heterogeneous watershed would create a progression of species emerging over a wider span of time.

When richness was regressed against abundance, the residual values for both canopy-cover and canopy-absence were similar, indicating that true richness was unaffected after ten years following canopy removal. Anderson (1992) noted that disturbance associated with clearcutting is characterized by a community structure dominated by a few very abundant species. Anderson (1992) found that only four species in clearcuts, versus 10 species in old-growth, comprised 50% of the biomass. We found similar trends in our study. Two genera of EPT *(Rhyacophila* sp., *Dicosmoecus* sp.) had the largest biomass and comprised 47% of the total EPT abundance emerging from streams flowing through early regeneration. In streams flowing through mature forest, *Rhyacophila* sp. and *Doroneuria* sp. had the highest biomass but comprised only 23% of the total abundance. The two most abundant genera emerging from streams flowing through young regenerating forests *(Malenka* and *Cinygma)* comprised 44% of the total; the two most abundant genera emerging from forested streams *(Malenka* and *Paraleptophlebia)* comprised only 29%.

The lack of statistical significance in the differences of emerging adult EPTs between streams flowing through 10-year-old regeneration and mature forest stands may simply be attributable to the high variability in the insect communities among watersheds (Moldenke and Ver Linden 2007) and the ability ofthese watershed systems to recover rapidly from disturbance.

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