AN ABSTRACT OF THE THESIS OF

<u>Charles H. Frady</u> for the degree of <u>Master of Science</u> in <u>Fisheries Science</u>
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Title: <u>Headwater Stream Macroinvertebrates of the H.J. Andrews Experimental</u>
<u>Forest, Oregon</u>

Abstract approved:

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Recent studies of headwater streams have demonstrated their

importance to overall watershed biodiversity, nutrient cycling, and energy flux.

However, little attention has been paid to long-term effects of forest harvest on

macroinvertebrate communities in headwater streams. This study investigated

headwater stream macroinvertebrate communities in the H.J. Andrews

Experimental Forest, Oregon, U.S.A and used a paired-stream study design to

examine the effect of prior forest harvest on stream macroinvertebrates.

Concomitantly, this study examined how macroinvertebrate life-history traits

were related to stream size, substrates, discharge, or water temperature.

Results from this study suggest that neither richness nor densities

differed between streams flowing through young growth versus old growth

forests. Despite similarities among these metrics, multivariate ordination

techniques helped elucidate differences in benthic community composition

between paired streams when red alder was present in riparian zones of

previously harvested basins. Indicator Species Analysis of community

composition and abundance revealed that no taxa were exclusively indicative of either forest type.

Macroinvertebrate life-history traits among headwater streams were related to stream size, stream substrates, or stream discharge. As predicted, macroinvertebrates that ingest leaf litter (shredders) decreased proportionally with increasing stream width, while macroinvertebrates that scrape off algae and biofilms from instream substrates (scrapers) increased with increasing stream width. Differences in macroinvertebrate habit-trait groups were related to differences in stream substrates or stream discharge between very small headwater streams (< 20ha basin area) and larger headwater streams (50-100ha basin size). Seasonal variation in stream discharge also influenced macroinvertebrate communities.

Patterns in adult insect emergence in these streams displayed pulses of activity that varied among streams. During summer 2003, total emergence was greatest in one high elevation stream in this study. During spring 2004, total emergence began earlier in one low elevation and one mid elevation stream, but linkages with stream water temperature were tenuous; cumulative emergence remained higher in these streams than all others through early summer 2004.

Though forest harvest often has immediate effects on macroinvertebrate communities, shifts in community composition may persist long-term if regrowth of riparian vegetation includes red alder (*Alnus rubra*). Analyses of macroinvertebrate life-history traits provided insight regarding species

adaptations to environmental conditions. Among six headwater streams within a relatively small landscape (6400ha), proportions of stream macroinvertebrate communities with specific traits differed among streams relative to variability in physical stream attributes.

Headwater Stream Macroinvertebrates of the H.J. Andrews Experimental
Forest, Oregon

by

Charles H. Frady

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"All there is to thinking…is seeing something noticeable which makes you see something you weren't noticing which makes you see something that isn't even visible."

- Norman Maclean, *A River Runs Through It*

CHAPTER 1: Introduction

Headwater streams in the central Cascade Mountains often contain high taxa richness and densities of stream macroinvertebrates (Progar and Moldenke 2002, Herlihy et al. 2005). The composition and abundance of these macroinvertebrate communities are influenced by multiple factors and can be used to examine the magnitude of natural and anthropogenic disturbances within the stream, as well as for adjacent hillslopes (Resh et al. 1988, Gregory et al. 1991).

Headwater stream ecosystems are important to stream and forest management because they comprise the majority of stream length in most montane stream networks in western North America (Sidle et al. 2000, Muchow and Richardson 2000, Gomi et al. 2002). Headwater streams are tightly coupled with physical and biological processes that occur in surrounding riparian areas (Vannote et al. 1980, Gregory et al. 1991). Biologically, riparian zones exhibit unique and diverse assemblages of both plants and animals (Naiman et al. 1993, Sabo et al. 2005). Function and connectivity of streams and riparian zones is important in nutrient cycling, sediment movement, and plant and animal dispersal (Gregory et al. 1991). In stream networks, headwater streams often supply downstream reaches with nutrients and food resources for higher organisms including fish (Vannote et al. 1980, Gomi et al. 2002, Wipfli and Gregovich 2002). These potential relationships between headwater and downstream reaches, as

well as aquatic and terrestrial interfaces, suggest headwater streams are important contributors to watershed biodiversity, nutrient cycling, and energy flux.

Despite their potential importance for stream connectivity, many headwater streams are not represented on 1:24000 maps (Meyer and Wallace 2001). These omissions contribute to difficulties in managing headwater streams (Moore and Richardson 2003). In the Pacific Northwest, stream regulations are often driven by distributions of fish, particularly salmonids. Harvest practices near non-fish bearing streams on state forest lands in the Pacific Northwest can include complete canopy removal even in riparian zones (Young 2000).

Removal of forest canopies has immediate impacts on terrestrial ecosystem processes and dynamics such as carbon cycling and sequestration (Cooper 1983, Harmon et al. 1990, Harmon 2001). Not only are terrestrial ecosystems affected by forest harvest, but stream ecosystems in the western Cascade Range of Oregon display shifts in physical and biological attributes in response to forest harvest including increased stream water temperature (Johnson and Jones 2000), increased water yield (Harr et el. 1975, Hicks et al. 1991), increased algal/biofilm biomass (Murphy et al. 1981, Fuchs et al. 2003, Hernandez et al. 2005), and allochthonous input losses (Bilby and Bisson 1992, Bisson and Bilby 1998) immediately post harvest.

In the first few years immediately following forest harvest, canopy shading is reduced and autochthonous (algae, diatoms, etc.) inputs may serve as the primary resource supporting macroinvertebrate communities (Triska et al. 1982, Webster et al. 1983, Gregory et al. 1987). These changes can affect

macroinvertebrate biodiversity (Newbold et al. 1980, Murphy and Hall 1981, Stone and Wallace 1998), densities (Newbold et al. 1980, Murphy et al. 1981, Hernandez et al. 2005), or community composition (Newbold et al. 1980, Hawkins et al. 1982, Stone and Wallace 1998, Hernandez et al. 2005).

Concomitant with natural or anthropogenic-induced changes, seasonal variation in physical stream conditions provides impetus for life-history adaptations among stream macroinvertebrates (Anderson and Wallace 1984, Poff and Ward 1989). As water temperature, incoming light levels, stream flow, and food resources vary with season, macroinvertebrates display adaptations in feeding plasticity, mode of existence, and timing of adult emergence. In particular, some stream macroinvertebrates display egg diapause to avoid suboptimal environmental conditions; hatching often occurs with increases in ambient moisture or stream flow (Anderson and Wallace 1984, Dieterich and Anderson 1995, Richardson 2001). These adaptations favor resistance and resilience in changing environments (Dudley and Anderson 1987, Friberg and Jacobsen 1994). Behavior of macroinvertebrates may also be influenced by changes in environmental conditions. Hyporheic zones (Stanford and Ward 1993) are used by some macroinvertebrates as refugia during both high flow spates (Townsend 1989) and dry periods (Williams and Hynes 1974, Griffith and Perry 1993).

Because anthropogenic changes to the environment often cause shifts in assemblages of natural communities (Loreau et al. 2001), knowing how ecosystem processes affect and ultimately maintain or reduce biodiversity is

important (Ricklefs 1987, Gessner et al. 2004, Giller et al. 2004). Increased biodiversity can influence energy transfer and nutrient processing in aquatic ecosystems such as leaf decomposition (Jonsson and Malmqvist 2000) and carbon dioxide flux (Morin and McGrady-Steed 2004).

The objective of this thesis was to explore biological responses of stream macroinvertebrates to 1) long-term changes in riparian vegetation following forest harvest and 2) variability in local stream attributes. This study examined benthic and emergent macroinvertebrate communities in three streams flowing through basins 20-40 years following forest harvest and compared them to communities in three streams flowing through old growth forests in the H.J. Andrews Experimental Forest, Oregon, U.S.A. One chapter examined the influence of forest type on macroinvertebrate richness, densities, and community composition during four seasons, from summer 2003 through spring 2004. The next chapter described the extent to which macroinvertebrate community composition, grouped by life-history traits, corresponded to local stream conditions in headwater streams.

CHAPTER 2: Seasonal dynamics of headwater stream macroinvertebrate communities: comparisons of streams through young growth and old growth forests.

INTRODUCTION

Forested headwater streams typically rely on riparian allochthonous resources (leaves, needles, catkins, etc.) as the food base for aquatic macroinvertebrates (Kaushik and Hynes 1971, Anderson and Sedell 1979, Cummins and Klug 1979, Vannote et al. 1980, Cummins et al. 1989). Differences in the structure and composition of riparian vegetation can influence allochthonous inputs and ultimately macroinvertebrate communities (Vannote et al. 1980, Anderson 1992).

In the Pacific Northwest, riparian vegetation can be dominated by deciduous or coniferous species, or a combination of both vegetation types (Franklin and Dyrness 1973). Deciduous leaves with high nitrogen content entering the stream are higher quality resources for macroinvertebrates than coniferous needles (Petersen and Cummins 1974, Friberg and Jacobsen 1994). Both deciduous and coniferous allochthonous inputs are colonized by microbes and algae which increase resource quality for detritus feeding macroinvertebrates, particularly shredders (Kaushik and Hynes 1971, Anderson and Cummins 1979, Cummins and Klug 1979, Stout et al. 1993, Franken et al. 2005), but microbes colonize deciduous inputs more quickly than coniferous inputs (Sedell et al. 1975, Triska et al. 1982).

Riparian areas dominated by deciduous species such as red alder (*Alnus rubra*) typically have pulses of allochthonous leaf inputs primarily in autumn (Haapala et al. 2001) and non-leaf inputs (i.e. catkins) in late winter or spring (Harrington et al. 1994). In contrast, riparian areas where coniferous species dominate typically exhibit allochthonous inputs that occur more evenly throughout the year in lower quantities (Triska et al. 1984). As seasonality of riparian inputs to streams vary with vegetation type, stream macroinvertebrates likely respond to these seasonal changes.

Forest harvest can alter riparian vegetation and lead to changes from allochthonous to autochthonous dominated resources instream. In the first few years immediately following forest harvest, canopy shading is reduced and autochthonous (algae, diatoms, etc.) inputs may serve as the primary resource supporting macroinvertebrate communities (Triska et al. 1982, Webster et al. 1983, Gregory et al. 1987). In the Pacific Northwest, regrowth of riparian red alder occurs fairly rapidly following disturbance below 800m elevation (Harrington et al. 1994). As riparian trees reestablish, incoming solar radiation is reduced, and allochthonous inputs generally become important once again.

Shifts in physical and biological characteristics of stream ecosystems following removal of riparian vegetation can have immediate, though varied, impacts on macroinvertebrate communities. For example, benthic taxa richness or diversity in streams flowing through recently clearcut basins can be lower (Newbold et al. 1980), higher (Murphy and Hall 1981, Stone and Wallace 1998), or not different (Newbold et al. 1980, Anderson 1992, Price et al. 2003,

Hernandez et al. 2005) than streams flowing through old growth forests. In the period immediately following clearcut harvest, total abundance of benthic macroinvertebrate communities often increase (Newbold et al. 1980, Murphy et al. 1981, Hernandez et al. 2005) as changes in overall taxonomic or functional feeding group community composition occur (Newbold et al. 1980, Hawkins et al. 1982, Stone and Wallace 1998, Hernandez et al. 2005). In addition, densities and biomass of macroinvertebrates colonizing instream leaf packs may be higher in deciduous versus coniferous packs (Culp and Davies 1985, but see Richardson et al. 2004). Though many studies have examined immediate effects of canopy removal on macroinvertebrate communities, few studies have investigated long-term responses to forest harvest and if changes in riparian vegetation influence macroinvertebrate communities following riparian regrowth in headwater streams.

This study examined benthic and emergent macroinvertebrate communities in streams flowing through basins 20-40 years following forest harvest and compared them to communities in streams flowing through old growth forests in the H.J. Andrews Experimental Forest, Oregon, U.S.A. The objectives of this study were to determine 1) if benthic or emergent taxa richness, benthic densities, shredder densities, and emergent abundances were higher in streams where the surrounding conifer forest had been harvested two to four decades ago, and 2) if benthic or emergent community composition differed between forest types. Given that headwater streams undergo physical and

biological changes seasonally, this study also explored how taxa richness,

densities/abundances, and community composition varied among seasons.

METHODS

Study Sites

　　To assess benthic and emergent macroinvertebrate taxa richness,

densities/abundances, and community composition, six perennial headwater

streams were sampled seasonally in the H.J. Andrews Experimental Forest

(Fig. 2.1). Watershed 1 (WS-1) and Watershed 2 (WS-2) are adjacent basins at

lower elevations, New Belgium Creek (N.B.) and Anderson Creek are adjacent

basins at mid elevations, and Watershed 7 (WS-7) and Watershed 8 (WS-8) are

adjacent basins at higher elevations of H.J. Andrews (Table 2.1); adjacent basins

will be referred to as paired streams or stream-pairs. Each pair was comprised

of one stream through a basin of young growth conifer forest and an adjacent

stream through old growth conifer forest; streams through young growth forests

will be referred to as YG streams and streams through old growth forests will be

referred to as OG streams. Vegetation in two young growth basins (WS-1 and

N.B.) was clearcut logged in the 1960's and burned following harvest. The other

young growth basin (WS-7) had overstory thinning in two separate events in

1974 and 1984 (Table 2.1). All harvested basins were replanted following

harvest primarily with Douglas-fir. Study stream reaches (50m long) were

located upstream of stream gauges or access roads except for WS-2 which was
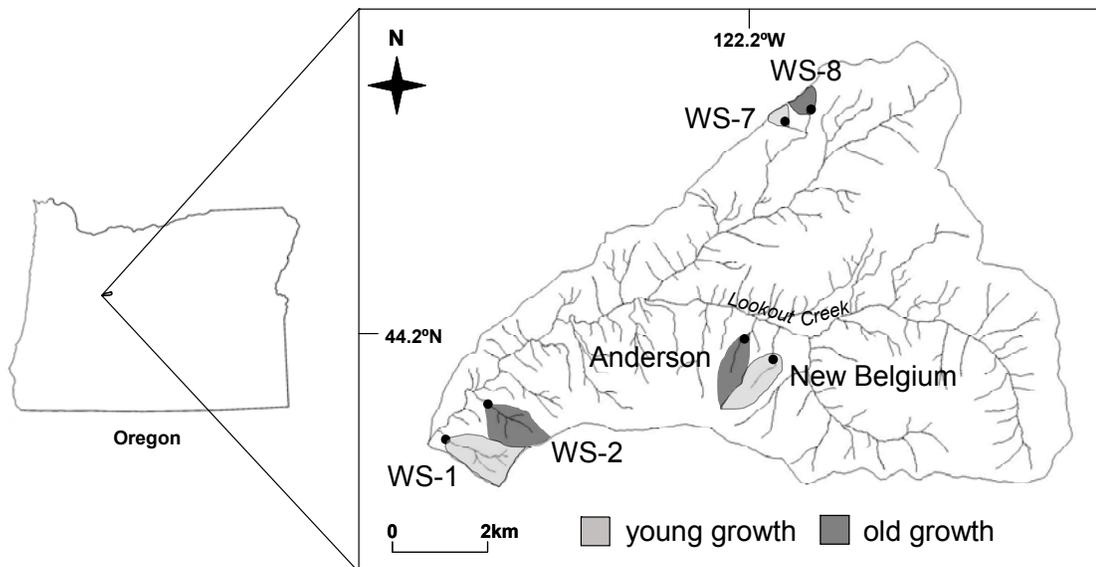
Fig. 2.1 Locations of headwater stream study basins in the H.J. Andrews Experimental Forest, Oregon, U.S.A. Study reaches are indicated by points (WS-2 study reach was located below stream gauge station).

Table 2.1 Physical characteristics of headwater stream study basins of the H.J. Andrews Experimental Forest. Elevation, stream width, and stream depth are study reach specific. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†) and WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*
Basin area (ha)	97.8	73.3	57.9	52.8	12.4	16.0
Elevation (m)	500	550	800	750	950	1000
Aspect	NW	NW	N-NE	N-NE	S-SE	S
Forest age (years)	40	450+	38	450+	20-30*	450+
Stream width (m)						
summer	1.9	2.1	1.2	1.9	1.2	1.1
autumn	2.3	3.0	1.8	2.4	1.6	1.6
winter	2.8	2.5	2.3	2.7	1.6	1.9
spring	2.0	2.3	2.1	2.4	1.3	1.8
Stream depth (cm)						
summer	7.1	8.8	4.4	4.6	2.6	2.7
autumn	18.4	15.3	13.6	11.0	6.0	7.1
winter	19.9	16.1	10.4	12.3	4.7	7.9
spring	13.6	8.2	8.5	8.3	4.3	4.7

*overstory vegetation in WS-7 was removed in two separate events (1974 and 1984)

located below the stream gauge.

H.J. Andrews Experimental Forest is located in the central Cascade Range of Oregon, U.S.A. and is characterized by steep topography and a maritime climate. There is a mosaic of uneven age conifer forests including old growth forests (400-500 years), mature stands (100-150 years), and young growth areas (<60 years). Natural wildfires, landslides, floods, and windthrow were the primary mechanisms responsible for this landscape heterogeneity before the onset of anthropogenic forest alterations.

Overstory riparian vegetation in headwater streams flowing through old growth forests in this study consisted primarily of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) (personal observations, Table 2.2). Riparian understory species in these areas included vine maple (*Acer circinatum*), pacific yew (*Taxus brevifolia*), red huckleberry (*Vaccinium parvifolium*), devil's club (*Oplopanax horridus*), and young conifer. Overstory riparian vegetation in previously harvested headwater basins in this study typically included red alder (*Alnus rubra*) and big leaf maple, with some black cottonwood (*Populus trichocarpa*) at the low elevation stream (personal observations, Table 2.2); in the high elevation stream subject to prior forest harvest (WS-7), red alder was very sparse and the riparian zone was dominated by young conifer and dense patches of vine maple. Riparian understory species in these areas included vine maple, ferns, devil's club, and young conifer.

Table 2.2 Presence (+) of riparian tree species in H.J. Andrews headwater stream study reaches. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†). WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

common name	latin name	WS-1†	WS-2*	N.B.†	Anderson*	WS-7†	WS-8*
big leaf maple	*Acer macrophyllum*	+		+			
black cottonwood	*Populus trichocarpa*	+					
Douglas-fir	*Pseudotsuga menziesii*	+	+	+	+	+	+
Pacific yew	*Taxus brevifolia*		+		+		+
red alder	*Alnus rubra*	+		+			
vine maple	*Acer circinatum*	+	+	+	+	+	
western hemlock	*Tsuga heterophylla*		+		+	+	+
western red cedar	*Thuja plicata*		+		+	+	+

Macroinvertebrate collections and laboratory procedures

Benthic macroinvertebrate sampling was conducted seasonally beginning June 2003 through May 2004 (Table 2.3). Summer benthic samples were collected in late June before stream flow was too low to sample with a Surber sampler. Autumn samples were collected in late November after stream flow returned to levels high enough to provide flow through the sampling net. Winter and spring samples were collected during periods of relatively stable stream flow, avoiding rain events (early March and May, respectively). Emergence samples were collected twice each season and traps were set for 6-8 days per sampling period (Table 2.3).

Six benthic samples and four emergence samples were collected in each 50m study reach each sampling period. Benthic sample locations were randomized each sampling period but emergence sample locations were randomized once at the onset of sampling. Benthic macroinvertebrates were collected with a 0.25mm mesh Surber sampler (0.093 m^2) only in riffle/cascade stream units on substrates ranging from silt to cobble. Emergence samplers consisted of pvc frames covering 0.25 m^2 stream bed draped with 0.6mm mesh nets. A small amount of unscented, biodegradable soap was added to the water in emergence trap collecting cups to decrease surface tension; in cold weather, rock salt was added to serve as both an antifreeze and preservative agent. All samples were stored in 95% ethanol.

Benthic and emergent insects were identified to genus when possible (Brown 1972, McAlpine et al. 1981, Stewart and Stark 1993, Merritt and

Table 2.3 Benthic and emergence sample collection periods.

season	benthic	emergence
summer 2003	June 19-24	June 24-30 July 10-16
autumn 2003	Nov. 30 - Dec. 1	Sept. 25 - Oct. 2 November 7-14
winter 2004	March 5-6	December 23-31 March 6-13
spring 2004	Apr. 30 - May 1	April 4-11 May 2-9

Cummins 1996, Wiggins 1996). Individuals of the family Chironomidae were identified to sub-family or tribe in benthic samples, and family level in emergence samples. Non-insects were typically identified to order (Thorp and Covich 1991). Young-instar insects and individuals damaged during sampling or storage were identified to the lowest taxonomic resolution possible, typically order or family. All individuals in each sample were identified, and benthic macroinvertebrates were assigned to functional feeding groups when possible (Merritt and Cummins 1996, Wiggins 1996).

Instream and riparian characterizations

Instream and riparian attributes were characterized each season beginning June 2003. Six transects were established perpendicular to stream flow at every 10m along stream reaches (including 0m as the first transect). Wetted stream widths were measured at these transects; stream depths and substrate type were characterized at 11 points across each transect (0%, 10%, 20%, ….100% of stream width). Substrate type was characterized by size as silt, sand, gravel, cobble, boulder, bedrock, small wood (<10cm diameter), or large wood (>10cm diameter) (modified from Wolman 1954). Substrate data was pooled from individual transects and calculated as stream reach totals.

Percent canopy cover was measured using a canopy densiometer mid-channel at each transect facing upstream, downstream, right bank, and left bank (Platts et al. 1987). Allochthonous litterfall was collected continuously between July 2003 and October 2003. Litter traps consisted of circular laundry baskets

(0.125 m^2) with 0.6mm mesh nets. To characterize major patterns in litterfall, six litter traps per stream were located under dominant overstory and understory vegetation; dominant riparian species were assessed visually. Leaf litter was collected monthly, dried at 60 ºC for 24-36 hours, and weighed. Litter was categorized as red alder leaves, other deciduous leaves, deciduous reproductive structures (catkins, samaras, etc), coniferous needles, coniferous cones, or miscellaneous (bark, lichen, moss, twigs, and wood).

Statistical Analyses

    Benthic and emergent taxa richness was calculated as a sum of all taxa per stream each season. For emergence samples, each richness value was a sum of taxa collected per stream during two sampling periods within each season (Table 2.3). Benthic and emergent richness totals, as well as benthic and shredder densities, were natural log (ln) transformed before parametric analyses. Emergent abundance data were square root transformed before parametric analyses. Transformations were made because data sets exhibited unequal variance of residuals. Differences between paired streams (young growth vs. old growth) in benthic or emergent taxa richness, benthic densities or emergent abundances within each season were tested with one-way ANOVA (SAS v.9.1); stream-pair was used as a random blocking factor.

    Benthic and emergent macroinvertebrate communities from all seasons were compared with Non-metric Multi-dimensional Scaling (NMS) (Kruskal 1964, Mather 1976) (PC-ORD 4 software, McCune and Mefford 1999). NMS is a non-

parametric ordination technique designed to analyze non-normal, heterogeneous data using a rank-transformation on Sørenson (Bray-Curtis) distances between samples (McCune and Grace 2002). It is an indirect gradient analysis which does not constrain ordinations by measured environmental variables; thus gradients and differences among overall communities are detected based on the communities themselves. Benthic data were $\log_{10}(x + 1)$ transformed to reduce differences in overall benthic densities. Presence/absence was used for emergent data instead of emergence rates (No. individuals m^2 day^{-1}) because emergence values were very patchy and ordination solutions were greatly influenced by extreme outliers. This study used Indicator Species Analysis to determine which taxa were strongly correlated to forest type or season (Dufrene and Legendre 1997, PCORD4 software). This technique creates indicator values (from 0 to 100, 100 being a perfect indicator) for all taxa by combining values of relative abundance and relative frequency; significance of group membership was determined through 1000 Monte Carlo simulations. Because statistics often obscure biologically meaningful differences, results from benthic Indicator Species Analysis were filtered recognize strong indicators if 1) they were represented in at least two of three streams of each forest type, 2) they were collected in at least two seasons, and 3) at least 25 total individuals of a given taxa were collected (only for benthic indicators). Numbers of individuals were not relevant for emergent indicators because analyses were performed on presence/absence data.

RESULTS

Study site characterizations

Canopy cover was highly variable among seasons in YG streams, and was less variable among seasons in OG streams (Table 2.4). Canopy cover was lower in YG streams than paired OG streams in both autumn and winter (Table 2.4), but among YG streams, it did not vary as much seasonally in WS-7 than in WS-1 and N.B. Most streams had substrates dominated by gravel and cobble (Table 2.5), but sand and silt generally comprised higher proportions in WS-7 and WS-8 than other streams (Table 2.5). WS-8 generally had higher proportions of both large and small wood substrates than other streams (Table 2.5).

In most months, litterfall biomass was similar between YG streams and OG streams, but in October biomass was greater near two YG streams than paired OG streams (Fig. 2.2). October litterfall biomass was approximately three times higher near YG streams at low and mid elevations (Fig. 2.2) where a substantial portion of litterfall collected were red alder leaves. Red alder leaves were never collected near OG streams.

Taxa richness

Benthic taxa richness was generally higher, though not significantly, in YG streams than OG streams in summer and spring (Table 2.6). In only two instances, benthic taxa richness was higher in an OG stream than its paired YG

Table 2.4 Mean study reach canopy cover (%). Canopy cover CV = coefficient of variation (stdev/mean*100) among seasons. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†). WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*
Canopy cover (%)						
summer	97.5	96.6	98.3	86.5	82.6	93.4
autumn	44.6	85.5	45.3	77.9	63.2	89.2
winter	36.8	77.5	45.6	70.6	65.0	89.2
spring	95.8	95.1	92.9	86.8	59.3	83.6
CV (%)	47.3	10.1	41.2	9.6	15.3	4.5

Table 2.5 Mean substrate composition (%). Values are average proportions across seasons. Values in parentheses are standard errors. Substrate type categories modified from Wolman 1954. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†). WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

substrate type	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*
silt	1.1	0.0	0.8	3.4	11.4	2.3
	(0.4)	(0.0)	(0.8)	(1.7)	(4.1)	(1.8)
sand	12.9	4.2	15.2	10.6	13.3	15.9
	(3.4)	(1.4)	(1.1)	(3.2)	(1.1)	(3.8)
gravel	37.9	53.0	39.0	37.1	51.1	42.0
	(6.4)	(5.3)	(2.9)	(3.2)	(9.1)	(4.5)
cobble	30.3	26.5	33.0	22.7	15.5	6.8
	(1.1)	(2.9)	(4.2)	(1.9)	(1.7)	(1.9)
boulder	9.5	11.4	7.2	6.4	4.5	2.7
	(2.5)	(2.7)	(0.7)	(1.0)	(3.1)	(0.9)
bedrock	7.2	1.9	2.3	16.7	1.5	15.2
	(0.7)	(1.9)	(2.3)	(0.0)	(1.5)	(0.9)
large wood[a]	0.0	0.0	1.1	1.1	1.1	4.5
	(0.0)	(0.0)	(1.1)	(0.4)	(0.7)	(2.2)
small wood[b]	1.1	3.0	1.5	1.9	1.5	10.6
	(1.1)	(0.6)	(0.6)	(1.4)	(0.6)	(1.1)

[a]diameter ≥ 10cm
[b]diameter < 10cm
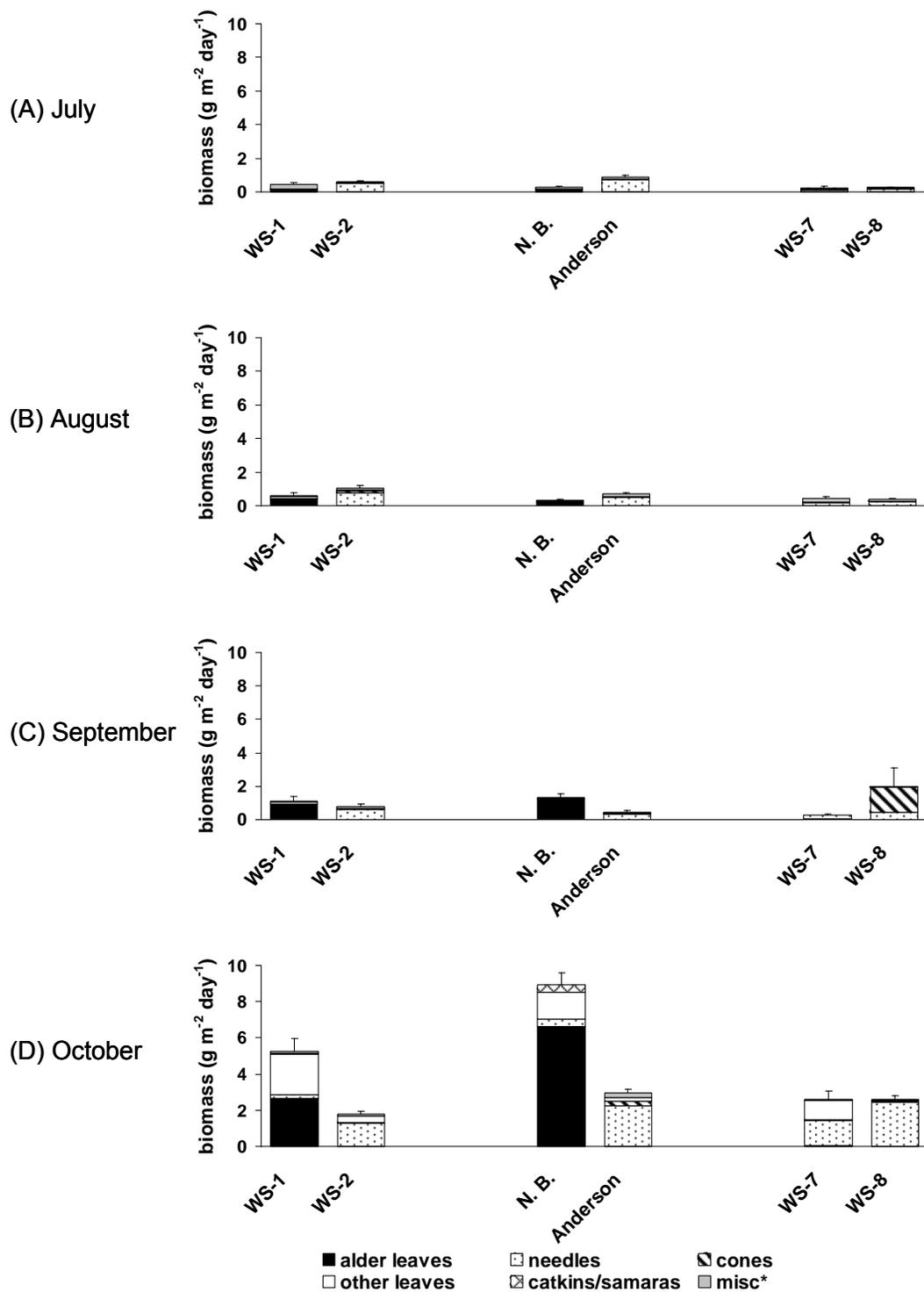
Fig. 2.2 Mean (+1 SE) litterfall biomass in (A) July, (B) August, (C) September, and (D) October. WS-1, N.B., and WS-7 are streams flowing through young growth forests. WS-2, Anderson, and WS-8 are streams flowing through old growth forests. *Misc. includes bark, lichen, moss, twigs, and wood.

Table 2.6 Taxa richness, benthic (and shredder) densities (No. individuals m^{-2}), and emergent abundances (No. individuals m^{-2} day^{-1}) by stream. Values in parentheses are standard errors. Values of benthic and emergent richness are aggregated stream totals; values of benthic (and shredder) densities and emergent abundances are stream means. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†); WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

response variable	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*	F stat	p value
Benthic richness								
summer	63	53	65	62	65	57	10.06	0.09
autumn	50	65	77	63	65	59	0.01	0.94
winter	55	53	59	71	56	54	0.25	0.66
spring	55	42	67	54	64	60	8.92	0.10
Emergent richness								
summer	25	17	32	31	38	38	1.27	0.38
autumn	9	11	7	8	11	8	0.00	0.98
winter	9	6	7	9	5	7	0.09	0.80
spring	25	21	24	23	16	14	8.99	0.10
Benthic densities								
summer	7188 (2048)	2510 (293)	10163 (2242)	10961 (3141)	8690 (2397)	6444 (865)	1.27	0.38
autumn	2196 (649)	5373 (935)	8460 (2415)	3905 (1006)	5425 (872)	4876 (789)	0.01	0.93
winter	5791 (643)	2045 (466)	5453 (778)	7965 (1558)	4232 (1241)	2506 (785)	1.08	0.41
spring	4429 (465)	1905 (289)	8978 (722)	5729 (627)	3640 (350)	3473 (517)	4.04	0.18
Shredder densities								
summer	866 (421)	402 (61)	2732 (643)	1114 (249)	1927 (681)	626 (166)	5.27	0.15
autumn	395 (145)	956 (213)	1308 (485)	434 (55)	895 (166)	640 (222)	0.02	0.89
winter	967 (247)	269 (121)	369 (92)	525 (172)	805 (285)	450 (193)	2.89	0.23
spring	718 (183)	251 (57)	1123 (130)	584 (141)	649 (77)	569 (153)	6.91	0.12
Emergent abundances								
summer	23.3 (5.3)	18.7 (2.4)	37.3 (4.4)	36.5 (4.4)	31.7 (6.2)	58.2 (11.8)	0.49	0.56
autumn	5.3 (1.6)	17.5 (6.0)	6.9 (1.4)	10.6 (4.2)	5.3 (1.0)	7.3 (2.3)	2.53	0.25
winter	4.9 (2.3)	2.2 (1.2)	3.5 (1.6)	2.0 (0.9)	2.0 (1.0)	1.8 (0.8)	0.87	0.45
spring	28.6 (10.4)	7.3 (1.9)	19.7 (3.8)	20.7 (8.5)	6.9 (1.3)	8.1 (2.8)	1.32	0.37

stream (Table 2.6). Though total taxa richness was similar between paired streams, some taxa were only found in one stream. Of the total benthic taxa collected in paired streams combined across all seasons, 61.9, 68.6, and 69.4% were similar between paired streams at low, mid, and high elevations, respectively. Rare benthic taxa occurred more frequently in YG streams; after pooling taxa in each stream across seasons, YG streams had on average 4.3 more unique taxa than paired OG streams (Appendix I). Benthic taxa richness did not reflect consistent seasonal trends across streams; peaks in richness among streams occurred in several different seasons.

Emergent taxa richness was similar between paired YG streams and OG streams every season (Table 2.6), and was generally higher in all streams in summer and spring than in autumn and winter (Table 2.6). Similar to patterns in benthic taxa richness, but to a greater degree, different emergent taxa occurred between paired streams. Of the total emergent taxa collected in paired streams combined across all seasons, only 56.2, 52.5, and 58.5% were similar between paired streams at low, mid, and high elevations, respectively. There were several emergent taxa unique to each stream after pooling taxa across all collection dates, but unlike patterns in benthic taxa rarity, YG streams did not always have more unique emergent taxa. Two YG streams (low and mid elevation) had on average 6 more unique emergent taxa than paired OG streams while the other YG stream (high elevation) had 4 fewer taxa than it's paired OG stream (Appendix II)

Total benthic and shredder densities

Total benthic macroinvertebrate densities were not significantly different between paired streams during any season (Table 2.6, Fig. 2.3). Total densities were highest in summer in five of six sites. Seasonal consistency was higher at high elevations where total densities were higher in the YG stream (WS-7) than its paired OG stream (WS-8) each season (Table 2.6, Fig. 2.3). At low elevations, total densities were higher in the YG stream (WS-1) than the corresponding OG stream (WS-2) in three of four seasons (Table 2.6, Fig. 2.3). At mid elevations, total densities were higher in the YG stream (N.B.) than its paired OG stream (Anderson) in only two seasons (Table 2.6, Fig. 2.3).

Though benthic shredder densities were not significantly different between paired streams in any season, shredder densities were generally higher in YG streams than paired OG streams (Table 2.6). Benthic shredders were commonly represented by numerous stonefly (Plecoptera) taxa including *Yoraperla* (Peltoperlidae: Plecoptera), early-instar Peltoperlidae, *Zapada* (Nemouridae: Plecoptera), early-instar Nemouridae, *Despaxia* (Leuctridae: Plecoptera), and *Moselia* (Leuctridae: Plecoptera) in streams through both forest types. Some benthic shredders were collected only in YG streams; these included *Chyranda* (Limnephilidae: Trichoptera), *Philocasca* (Limnephilidae: Trichoptera), *Prionocera* (Tipulidae: Diptera), *Pteronarcella* (Pteronarcyidae: Plecoptera), and *Tipula* (Tipulidae: Diptera). No benthic shredders were collected only in OG streams.
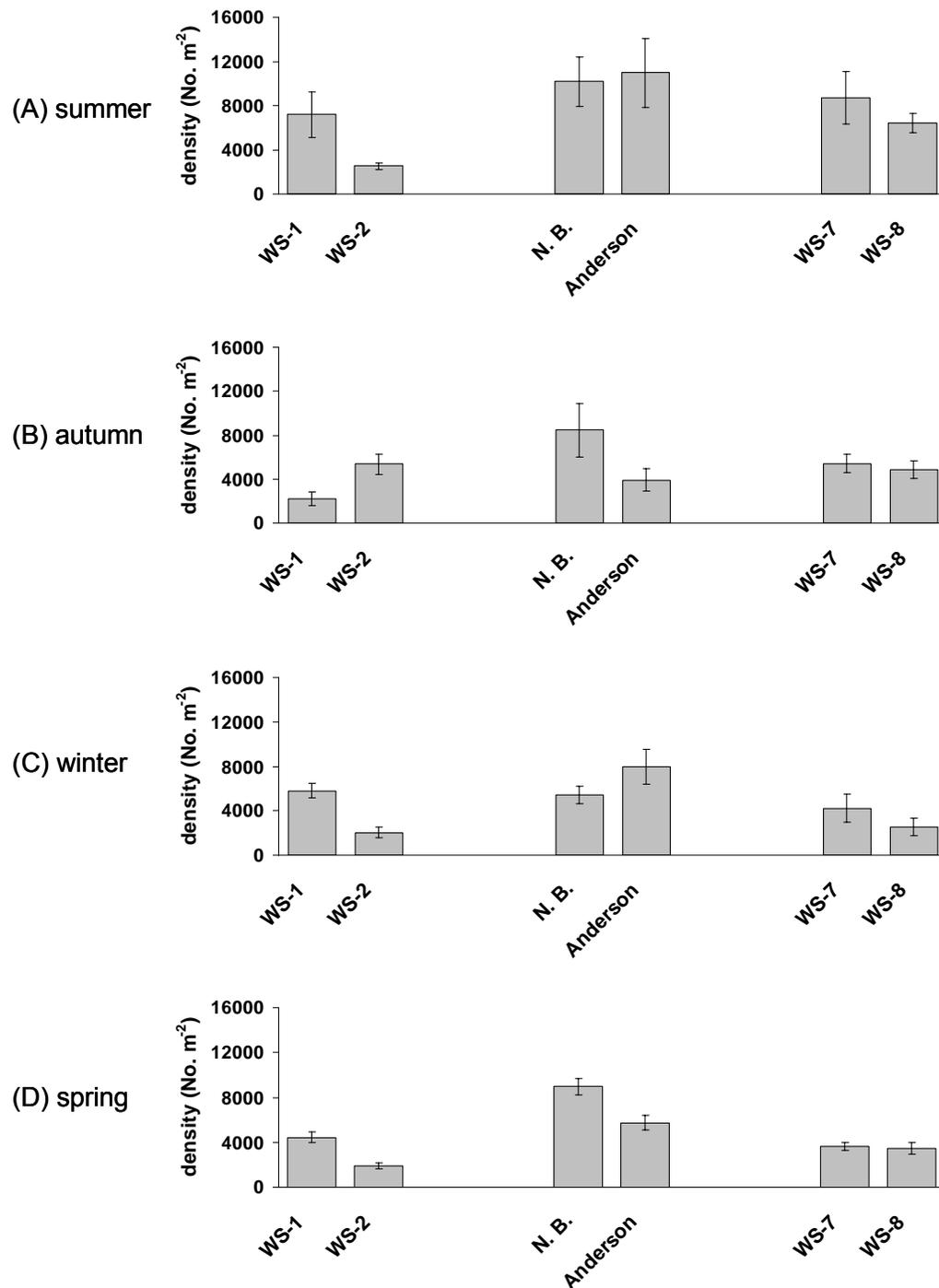
Fig. 2.3 Mean (±1 SE) benthic macroinvertebrate densities in (A) summer, (B) autumn, (C) winter, and (D) spring. WS-1, N.B., and WS-7 are streams flowing through young growth forests. WS-2, Anderson, and WS-8 are streams flowing through old growth forests.

Emergent abundances

Total emergent insect abundances were not significantly different between paired YG and OG streams in any season (Table 2.6), but trends within individual insect orders were detected. In summer, more Ephemeroptera emerged in mid and high elevation OG streams than YG streams, but more Trichoptera emerged in low and mid elevation YG streams than OG streams in the same season (Table 2.7). In autumn, more Plecoptera and Trichoptera emerged in all OG streams than YG streams (Table 2.7). In winter, more Diptera emerged in low and mid elevation YG streams than OG streams (Table 2.7). In spring, more Ephemeroptera emerged in all YG streams than OG streams while more Plecoptera emerged in low and mid elevation YG streams (Table 2.7). Diptera (predominantly Chironomidae and Chironomidae/Ceratopogonidae sp.) was the most abundant order in emergent communities, and accounted for the majority of emergence in summer (Table 2.7).

Community composition

When benthic community composition in all streams from all seasons was compared, differences in community composition between forest types were not visible in NMS ordination space (Fig. 2.4). Because benthic communities were visibly different among stream-pairs within the original ordination (Fig. 2.5), subsequent ordinations were calculated for individual stream-pairs. These ordinations revealed strong differences in benthic community structure between paired streams at low and mid elevations (Fig. 2.6A and B, respectively), but not

Table 2.7 Mean emergent abundances (No. individuals m^{-2} day^{-1}) by insect order. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†); WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

	WS-1†	WS-2*	N.B.†	Anderson*	WS-7†	WS-8*
Diptera						
summer	11.4	14.3	26.0	21.9	19.1	36.7
autumn	3.2	11.1	5.1	4.9	2.9	3.1
winter	3.7	0.9	2.5	0.8	0.5	0.6
spring	16.2	3.1	12.4	17.7	2.5	4.3
Ephemeroptera						
summer	6.7	2.3	3.3	8.5	2.9	6.4
autumn	0.1	0.9	0.0	0.1	0.7	0.0
winter	0.1	0.0	0.0	0.0	0.0	0.0
spring	7.8	0.5	1.9	0.8	0.4	0.1
Plecoptera						
summer	1.1	0.9	4.0	4.8	7.5	12.3
autumn	1.9	3.9	1.2	3.9	1.6	4.0
winter	0.6	0.3	1.0	0.7	1.0	1.2
spring	3.9	1.4	4.3	1.5	3.1	3.0
Trichoptera						
summer	3.9	1.1	3.8	1.3	2.2	2.7
autumn	0.0	1.6	0.6	1.7	0.1	0.2
winter	0.1	0.0	0.0	0.3	0.5	0.1
spring	0.3	0.9	1.0	0.6	0.9	0.7
Coleoptera & Hemiptera						
summer	0.3	0.0	0.1	0.0	0.0	0.1
autumn	0.0	0.0	0.0	0.0	0.0	0.0
winter	0.4	0.9	0.1	0.3	0.0	0.0
spring	0.4	1.4	0.0	0.1	0.0	0.0
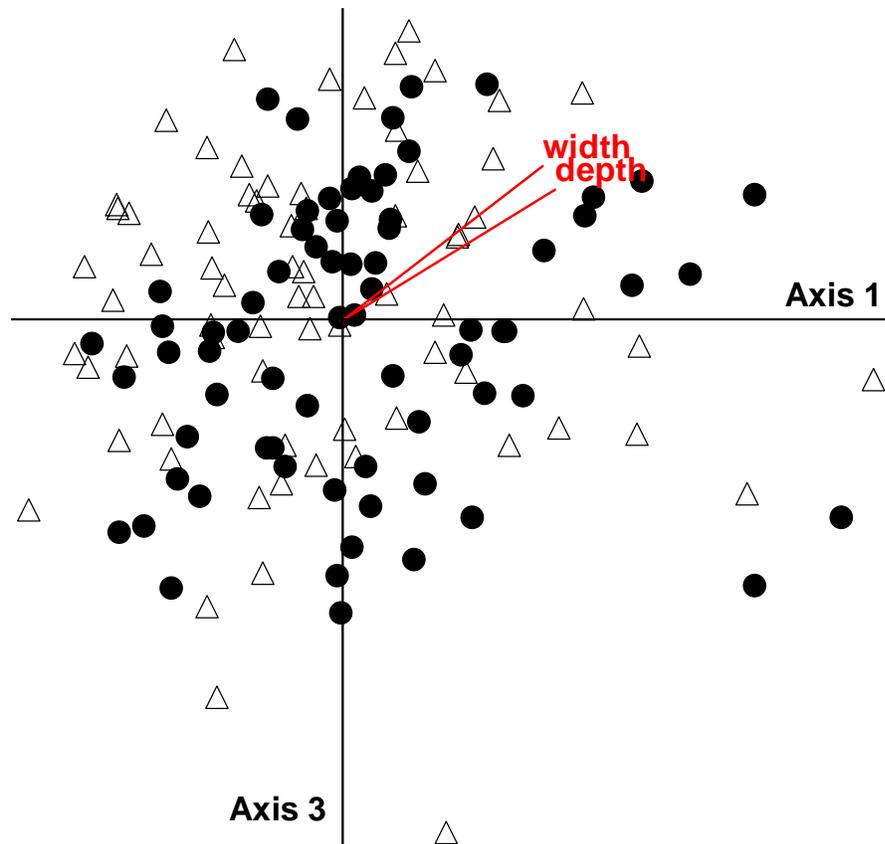
Fig. 2.4 NMS ordination of benthic macroinvertebrate communities across all streams rotated to compare forest types. (●) young growth, (△) old growth. Axis 1 r^2 = 0.323, Axis 3 r^2 = 0.237, final stress = 16.2, final instability = 0.0001. Vectors indicate physical measurements correlated with axes scores ($r^2 \geq 0.35$).
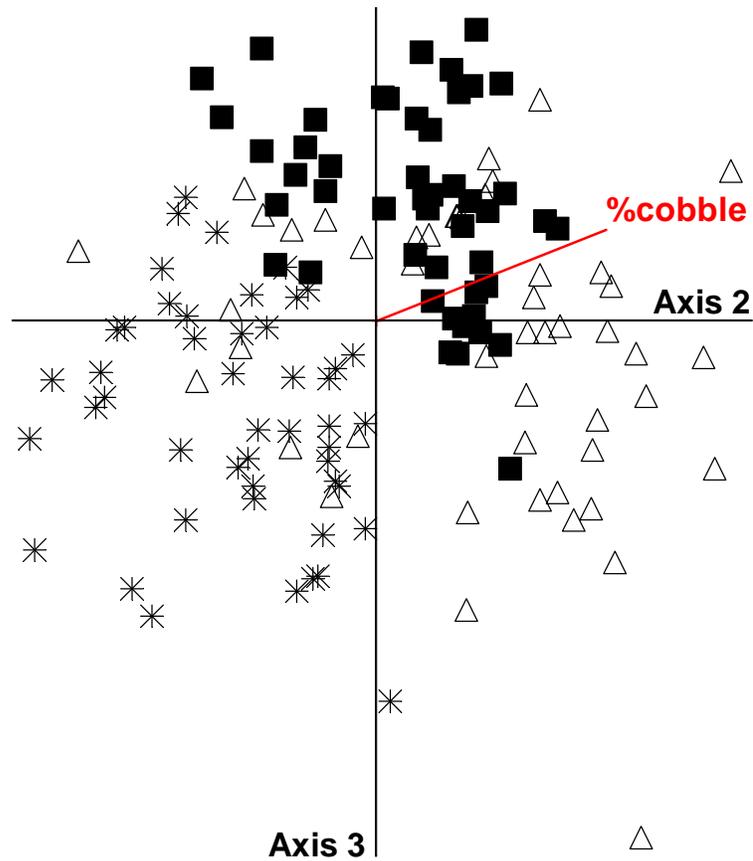
Fig. 2.5 NMS ordination of benthic macroinvertebrate communities across all streams rotated to compare stream-pairs. ($\triangle$) low elevation pair, ($\blacksquare$) mid elevation pair, ($\ast$) high elevation pair. Axis 2 r^2 = 0.254, Axis 3 r^2 = 0.237, final stress = 16.2, final instability = 0.0001; Vector indicates physical measurement (% cobble) correlated with Axis 2 scores ($r^2 \geq$ 0.35).
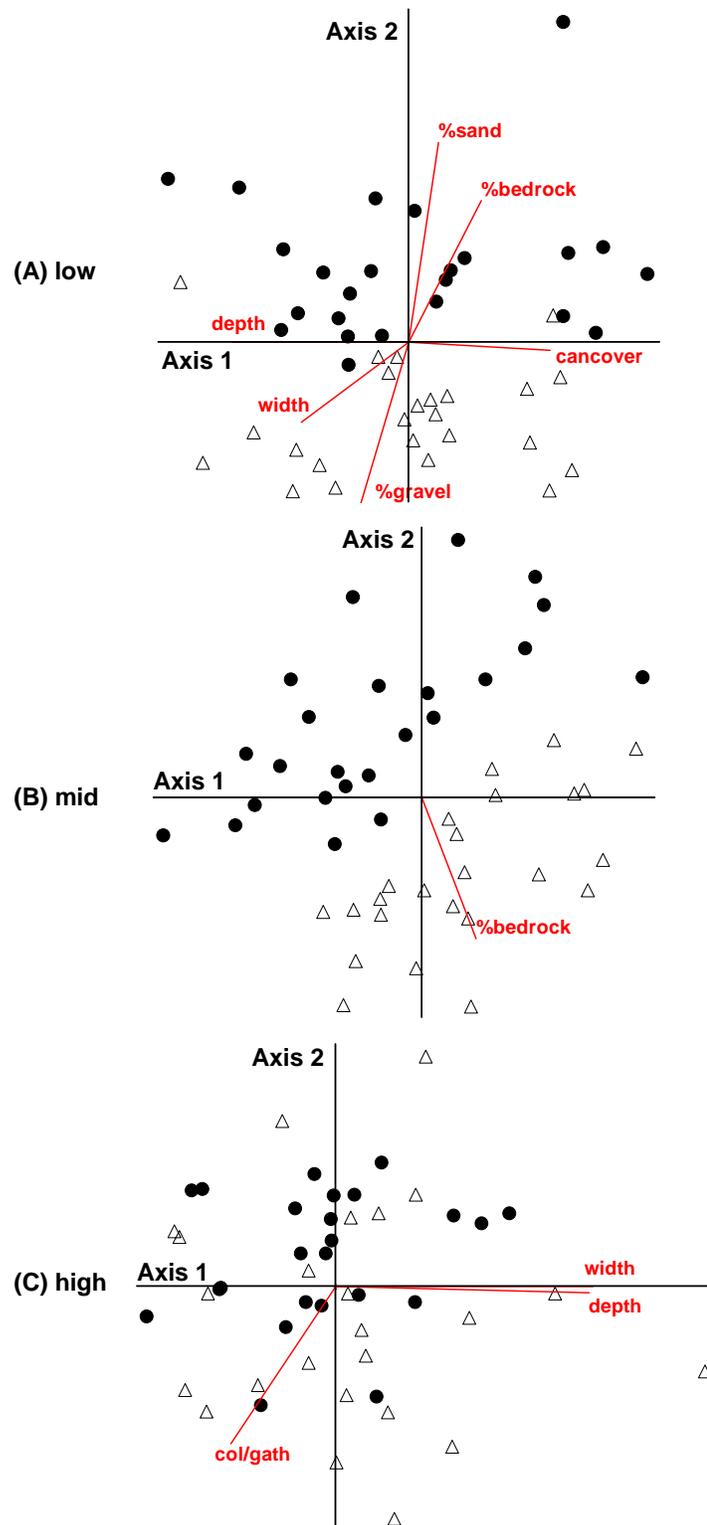
Fig. 2.6 NMS ordinations of benthic macroinvertebrate communities in (A) low, (B) mid, and (C) high elevation paired streams rotated to compare forest types. (●) young growth, (△) old growth. (A) Axis 1 r^2 = 0.412, Axis 2 r^2 = 0.213, final stress = 14.9, final instability = 0.00008; (B) Axis 1 r^2 = 0.221, Axis 2 r^2 = 0.224, final stress = 12.8, final instability = 0.0001; (C) Axis 1 r^2 = 0.395, Axis 2 r^2 = 0.236, final stress = 15.6, final instability = 0.00009. Vectors indicate physical measurements and functional feeding groups correlated with axes scores ($r^2 \geq 0.35$).

at the high elevation stream-pair (Fig. 2.6C). Percent sand and percent bedrock

substrates correlated with benthic communities in the low elevation YG stream

(Fig. 2.6A), while percent gravel substrates correlated with benthic communities

in the low elevation OG stream (Fig. 2.6A). In contrast, percent bedrock

substrates correlated with benthic communities in the mid elevation OG stream

(Fig. 2.6B).

Indicator Species Analysis determined 38 benthic taxa were significant (p

≤ 0.10) indicators of forest type (Appendix III). However, following strong

indicator guidelines, and considering strong statistical evidence ($p < 0.01$),

benthic indicators of YG streams included several collector-filtering taxa, early-

instars of one predacious stonefly family, one genus of predacious craneflies

(*Dicranota*), a subfamily of midges, an order of copepods, and roundworms

(Table 8). Benthic indicators of OG streams included two shredder genera, one

caddisfly (*Lepidostoma*) and one stonefly (*Visoka*) (Table 2.8).

Seasonal differences in benthic communities were visible in NMS

ordinations when all streams were combined (Fig. 2.7). Percent cobble substrate

was the only measured environmental variable modestly correlated ($r^2 ≥ 0.35$)

with benthic communities (Fig. 2.7); it was negatively correlated with samples

from autumn. Indicator Species Analysis also determined 82 benthic taxa were

significant ($p ≤ 0.10$) indicators of at least one season (Appendix III).

Ordinations of emergent insect communities revealed no differences

between forest types (Fig. 2.8). Unlike ordinations of benthic communities,

emergent communities did not show differences among stream-pairs, or between

paired streams. However, Indicator Species Analysis determined 7 emergent

taxa were significant ($p \leq 0.10$) indicators of forest type (Appendix IV). Following

strong indicator guidelines, emergent indicators of YG streams included midges,

one genus of mayfly (*Ironodes*), and one genus of caddisfly (*Rhyacophila*) (Table

2.8). Emergent indicators of OG streams included two genera of caddisflies

(*Anagapetus* and *Wormaldia*) (Table 2.8).

The most apparent differences in overall emergent communities were

among seasons (Fig. 2.9). Similar to benthic communities, emergent

communities demonstrated numerous taxa strongly associated with different

seasons. Indicator Species Analysis determined 52 emergent taxa were

significant ($p \leq 0.10$) indicators of at least one season (Appendix IV).

Table 2.8 Strong benthic and emergent indicators with associated Indicator Species Analysis values. Indicator values (% of perfect indication) were derived by combining values of relative abundance and relative frequency (Dufrene and Legendre 1997).

Benthic

Order	Family	Genus/Taxa	forest type	
			young growth	old growth
Corbiculaceae	Sphaeriidae	Sphaeriidae sp.	26	5
Diptera	Chironomidae	Orthocladiinae	52	48
	Simuliidae	Simuliidae sp.	42	15
		Simulium	19	1
	Tipulidae	*Dicranota*	39	12
Harpacticoida	Harpacticoida sp.	Harpacticoida sp.	52	36
Nematoda	Nematoda sp.	Nematoda sp.	51	30
Plecoptera	Nemouridae	*Visoka*	7	33
	Perlodidae	Perlodidae sp.	21	1
Trichoptera	Lepidostomatidae	*Lepidostoma*	13	45

Emergent

Order	Family	Genus/Taxa	young growth	old growth
Diptera	Chironomidae	Chironomidae sp.	49	39
Ephemeroptera	Heptageniidae	*Ironodes*	13	2
Trichoptera	Glossosomatidae	*Anagapetus*	0	6
	Philopotamidae	*Wormaldia*	4	22
	Rhyacophilidae	*Rhyacophila*	15	3
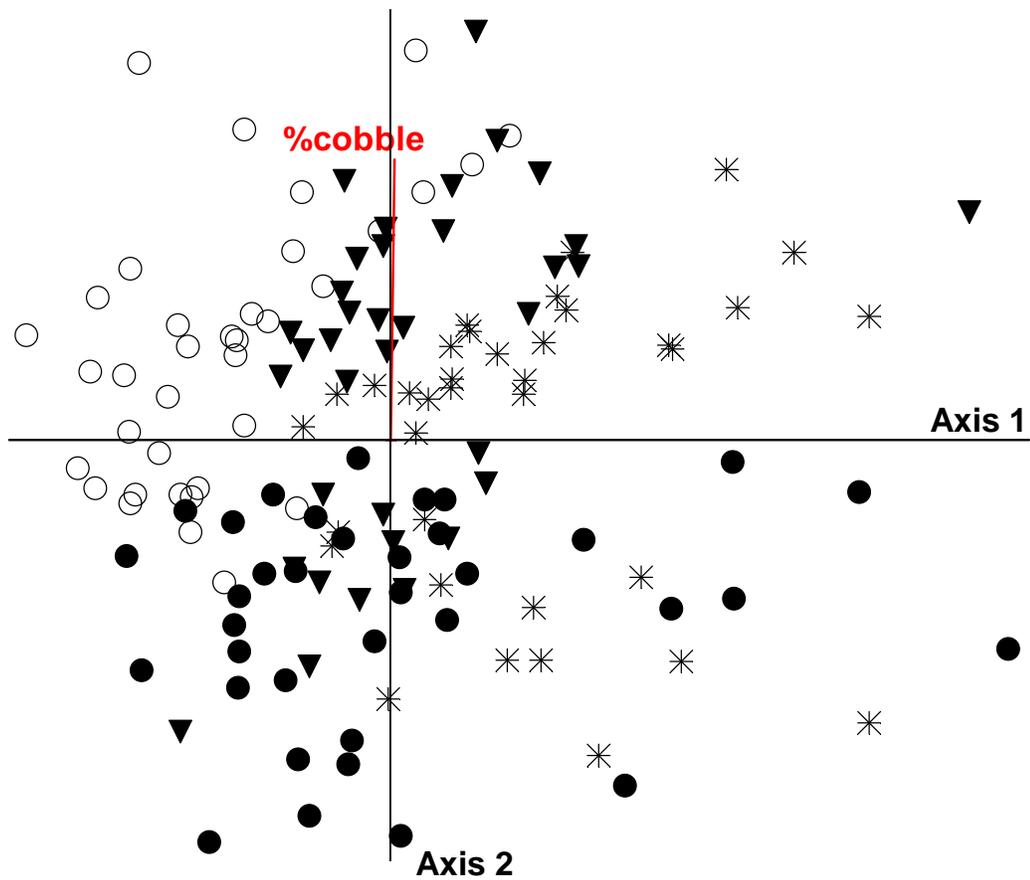
Fig. 2.7 NMS ordination of benthic macroinvertebrate communities across all
streams rotated to compare seasons. (○) summer, (●) autumn, (✳) winter, and
(▼) spring. Axis 1 r^2 = 0.323, Axis 2 r^2 = 0.254, final stress = 16.2, final instability
= 0.0001; Vector indicates physical measurement (% cobble) correlated with Axis
2 scores ($r^2 \geq 0.35$).
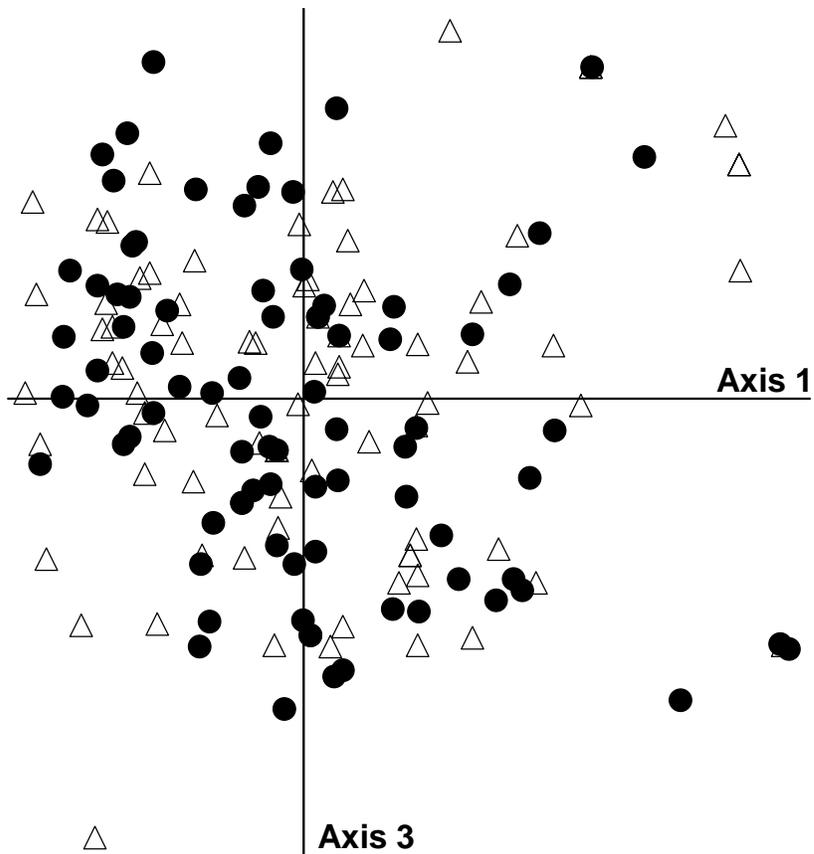
Fig. 2.8 NMS ordination of emergent insect communities across all streams rotated to compare forest types. (●) young growth, (△) old growth. Axis 1 r^2 = 0.321, Axis 3 r^2 = 0.179, final stress = 19.9, final instability = 0.00008.
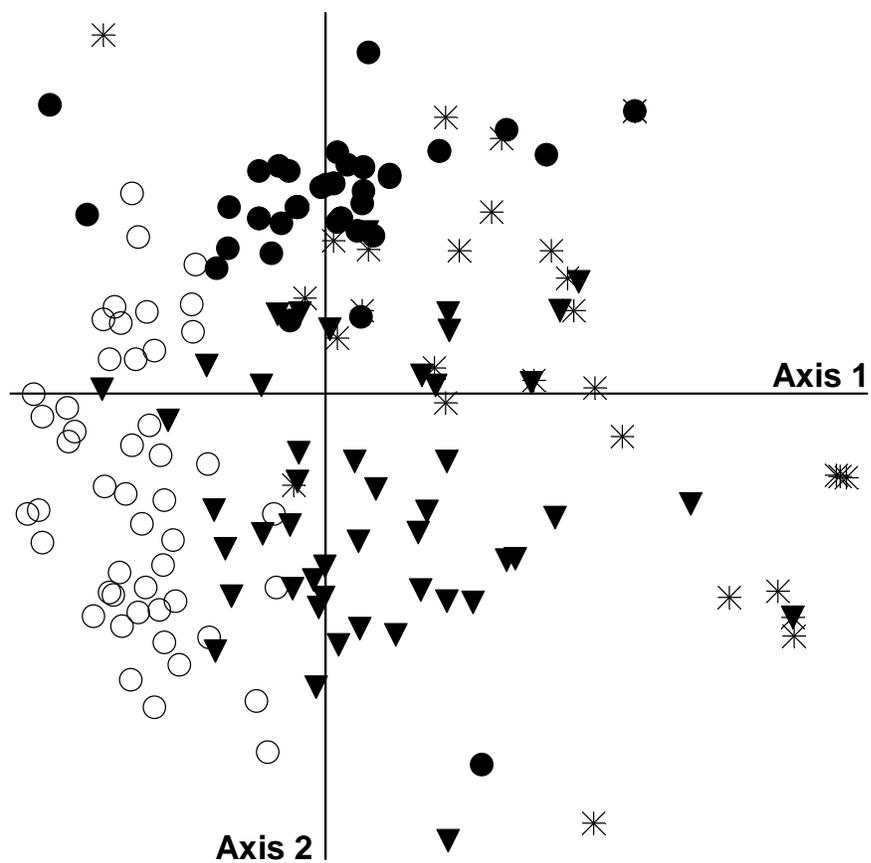
Fig. 2.9 NMS ordination of emergent insect communities across all streams rotated to compare seasons. (○) summer, (●) autumn, (✳) winter, and (▼) spring. Axis 1 r^2 = 0.321, Axis 2 r^2 = 0.229, final stress = 19.9, final instability = 0.00008.

DISCUSSION

Headwater streams flowing through young growth forests that were harvested 20-40 years ago had generally similar benthic and emergent taxa richness, benthic (and shredder) densities, and emergent abundances as paired streams flowing through old growth forests. These data suggest no long-term residual effects of forest harvest on macroinvertebrate biodiversity or densities in headwater streams of the H.J. Andrews Experimental Forest.

Though differences in macroinvertebrate community composition are often due to taxa only collected in one stream or a group of streams, this study found little evidence for any taxa that only occurred in streams flowing through either forest type. Despite the lack of indicators exclusive to one forest type, rigorous sampling efforts found differences in abundances and frequencies of numerous benthic and emergent taxa between forest types; these findings suggest that quantitative sampling is important in analyses of macroinvertebrate composition.

Overall community composition of benthic macroinvertebrates differed between paired YG and OG streams, but only when red alder was present in riparian areas of YG streams. The contributions of red alder inputs to streams are important in structuring benthic macroinvertebrate communities (Culp and Davies 1985, Piccolo and Wipfli 2002, Wipfli and Musselwhite 2004, Hernandez et al. 2005). Through nitrogen fixation, red alder may provide headwater stream macroinvertebrates with higher quality organic matter not found in streams without nitrogen fixing riparian vegetation.

Red alder did not grow in the YG stream at high elevation (WS-7) following forest harvest. Lack of red alder in this stream may help explain why overall benthic community composition was very similar between this stream and the adjacent OG stream (WS-8). Riparian vegetation composition in WS-7 may be a result of forest harvest thinning (60 percent of overstory vegetation was removed in 1974, with the remaining overstory removed in 1984). Vine maple was abundant in WS-7 but not in WS-8 yet this difference was not reflected in macroinvertebrate community composition. Similarities in community composition between these streams may have been more related to dominant stream substrates than riparian vegetation (Williams et al. 2002, Cole et al. 2003, Herlihy et al. 2005); substrates in these streams were generally finer than those in streams at low and mid elevations.

Since adult insect emergence is the culmination of juvenile development in streams, this study expected coherence of benthic and emergent communities. However, emergence sampling detected fewer differences in community composition between forest types than benthic sampling; emergence sampling collected only a fraction of the insect community that was emerging at a given time, whereas benthic sampling collected residents of the long-term ($\geq$ I year) macroinvertebrate community. Surprisingly, emergent insect communities demonstrated lower similarity in taxa collected between paired streams than did benthic communities, but fewer differences in community composition between paired streams.

Stream insects often emerge in response to environmental factors including photoperiod (Marten and Zwick 1989, Dieterich and Anderson 1995), temperature (Anderson and Cummins 1979, Short and Ward 1981, Sweeney and Vannote 1986), and variation in streamflow (Steedman and Anderson 1985, Dudley and Anderson 1987, Lytle and Poff 2004). Because emergence collections were not continuous throughout the year, rates of emergence and overall emergent composition from different collection periods may reflect behavior of stream insects to instantaneous environmental conditions.

Though deciduous vegetation is a highly nutritious resource for stream macroinvertebrates (Petersen and Cummins 1974, Cummins and Klug 1979, Cummins et al. 1989) that can influence benthic communities (Culp and Davies 1985, Piccolo and Wipfli 2002, Wipfli and Musselwhite 2004, Hernandez et al. 2005), the current study found little evidence of increased macroinvertebrate taxa richness and densities in relation to differences in riparian vegetation among streams. High species heterogeneity in riparian zones of old growth forests in H.J. Andrews Experimental Forest including well developed deciduous understories (Franklin and Dyrness 1973, Halpern 1987, Schoonmaker and McKee 1988) may provide stream macroinvertebrates with high quality resources similar to those found in riparian areas of young growth forests.

A study of headwater streams in southeastern Alaska found higher benthic taxa richness in "young alder" streams than streams flowing through old growth forests, but deciduous species in old growth understories may have been lacking (Hernandez et al. 2005). A study in and around H.J. Andrews Experimental

Forest reported a greater number of species emerging from a stream flowing through an old growth forest than from a stream flowing through a 40 year old deciduous forest (Anderson 1992); since this study performed nearly continuous sampling and identified insects to species, their findings suggest that persistent sampling and species-level identification may be important in detecting differences in biodiversity related to forest vegetation.

Results from the current study suggest peaks in headwater stream macroinvertebrate communities may not coincide with autumnal litterfall as do communities in larger streams (Murphy et al. 1981). However, benthic macroinvertebrates are capable of substantial trophic plasticity and likely feed on various in-stream resources from season to season (Friberg and Jacobsen 1994, Mihuc and Mihuc 1995, Mihuc and Minshall 1995, Mihuc 1997, Dangles 2002).

Benthic shredder densities in YG streams were frequently two times higher than in paired OG streams. In addition to potential effects of smaller stream size in comparison to previous studies (Hawkins et al. 1982), sampling technique may have influenced the magnitude of differences in benthic shredder densities between paired streams. In the current study, benthic macroinvertebrates were collected with 0.25mm mesh gear and young benthic shredders (e.g. early-instar leuctrid, nemourid, and peltoperlid stoneflies) were an abundant component of benthic densities in YG streams; on average, these taxa were 82 percent more abundant in YG streams than OG streams. These could have passed through a 1.0mm mesh net used in a previous study (Hawkins et al. 1982).

Many studies investigating macroinvertebrate response to forest harvest are conducted in only one season (Newbold et al. 1980, Noel et al. 1986, Brown et al. 1997, Cole et al. 2003, Fuchs et al. 2003, Herlihy et al. 2005, Hernandez et al. 2005) (but see Murphy et al. 1981, Hawkins et al. 1982, Stone and Wallace 1998, Kedzierski and Smock 2001). Seasonal sampling increased the total number of both benthic and emergent taxa collected and revealed strong seasonal differences in both benthic and emergent community composition. By identifying samples in their entirety, rare taxa contributed greatly to overall taxa richness which undoubtedly would have been underestimated with sub-sampling.

Results from this study are useful in understanding how differences in riparian vegetation can affect macroinvertebrate communities in headwater streams. However, differences between forest types were only found in analyses of benthic community composition and when riparian red alder was present in previously harvested basins. Because benthic macroinvertebrate sampling assesses the entire resident macroinvertebrate community at a given time (which may include long-lived taxa and non-insects), benthic collections may be more practical than emergence sampling in detecting patterns related to riparian vegetation.

Though prior studies have shown that macroinvertebrate taxa richness and densities in headwater streams are often influenced by clearcut forest harvest, these differences may only persist short-term. However, if riparian vegetation regrowth in previously harvested headwater basins includes red alder,

benthic macroinvertebrate community composition in these streams may exhibit

long-term compositional shifts.

CHAPTER 3: Influences of local stream conditions on macroinvertebrate life-history traits in headwater streams

INTRODUCTION

Historically, we have come to expect particular distributions of stream organisms and communities associated with temporal patterns of physical and biological stream characteristics (Vannote et al. 1980, Minshall et al. 1983, Townsend 1989). However, stream attributes vary across landscapes (Pringle et al. 1988, Hildrew and Giller 1994, Townsend et al. 2003). Because of intimate associations with terrestrial environments and geomorphic landscape features (Gregory et al. 1991), headwater stream communities likely adapt to specific stream conditions (Vannote et al. 1980, Huryn and Wallace 1987). Riparian and instream attributes that structure aquatic macroinvertebrate communities include riparian vegetation (Kaushik and Hynes 1971, Vannote et al. 1980, Cummins et al. 1989, Gregory et al. 1991), dominant stream substrates (Minshall and Minshall 1977, Riece 1980, Huryn and Wallace 1987), and stream discharge (Statzner et al. 1988, Hart and Finelli 1999). Additionally, stream temperature can affect growth and development of benthic macroinvertebrates (Anderson and Cummins 1979, Grafius and Anderson 1980, Short and Ward 1981, Sweeney and Vannote 1986).

The idea of partitioning stream macroinvertebrates into functional feeding groups came from understanding that various taxa acquire food in different ways (Cummins 1974, Cummins and Klug 1979). Some stream macroinvertebrates feed directly on allochthonous inputs by tearing off and ingesting pieces of

leaves, needles, etc.; these taxa have been identified as shredders. General stream ecosystem theory suggests that shredders are co-dominant in headwater streams along with collector gatherers (Vannote et al. 1980, Minshall et al. 1983), but because they feed on allochthonous leaf litter, shredders typically decrease proportionally in larger downstream reaches (Vannote et al. 1980, Minshall et al. 1983, Grubaugh et al. 1996). Scrapers rely heavily on autochthonous resources such as algae and bacteria that they scrape off stream substrates and tend to increase proportionally with the availability of these resources (Wiggins and Mackay 1978).

In addition to how stream macroinvertebrates acquire their food, life-history traits that determine where and how organisms survive are also useful descriptors of community structure (Hawkins 1984, Poff 1997, Usseglio-Polatera 2000, Lamouroux et al. 2004). Habit traits classify macroinvertebrates according to their modes of existence (Merritt and Cummins 1996); these traits have implications for which microhabitats organisms inhabit (Reice 1980, Hawkins 1984, Anderson and Wallace 1984, Fairchild and Holomuzki 2002) and for adaptations facilitating how they live in these microhabitats (Anderson and Wallace 1984, Statzner et al. 1988, Hart and Finelli 1999). Stream macroinvertebrate taxa that burrow into fine sediments and organic matter accumulations are burrowers, whereas taxa that live on surfaces of these substrates are sprawlers. Climbers typically move vertically on instream hydrophytes or on detritus. Clingers have adaptations (i.e. streamlined bodies, curved tarsal claws, production of silk as an attachment device) to live on

surfaces of larger inorganic substrates that are subject to high stream flows. Swimmers can swim short distances in stream channels.

Ontogenies of stream insects reflect temporal changes in microhabitat, and reach-specific, landscape, or regional differences in physical and biological environmental conditions (Power et al. 1988, Townsend 1989, Poff 1997, Lamouroux et al. 2004). Many taxa exhibit differences in developmental rates, onset of pupation, or timing of emergence based on changes in environmental conditions such as photoperiod (Marten and Zwick 1989, Dieterich and Anderson 1995), temperature (Anderson and Cummins 1979, Short and Ward 1981, Sweeney and Vannote 1986), and variation in streamflow (Steedman and Anderson 1985, Dudley and Anderson 1987, Lytle and Poff 2004). For example, in the central Cascade Range of Oregon, insect emergence was correlated with differences in temperature associated with elevation (Anderson 1992). Another study in western Oregon headwaters found differences in emergence timing between intermittent and perennial streams for several insect taxa possibly related to drying stream channels (Progar and Moldenke 2002).

Members of headwater communities have multiple strategies for adapting to resource availability and to changes in habitat. In the previous chapter, macroinvertebrate communities were compared between paired streams flowing through young growth and old growth forests. However, macroinvertebrate communities were variable among individual streams, and no strong differences between forest types were found when all streams were examined together. Relationships between macroinvertebrate communities and physical stream

attributes were not directly evaluated. The objectives of this study were to determine how macroinvertebrate communities were influenced by local stream conditions in headwater streams. This study evaluated patterns in benthic macroinvertebrate functional feeding groups and habit trait groups. Using these life-history traits, this study examined how macroinvertebrates responded to stream size, substrates, or discharge. Additionally, this study examined relationship trends between emergence timing and abundance with cumulative stream water temperature.

METHODS

Study sites

To assess benthic and emergent macroinvertebrate life-histories, six perennial headwater streams were sampled in the H.J. Andrews Experimental Forest (Fig. 2.1). Watershed 1 (WS-1) and Watershed 2 (WS-2) were streams at lower elevations (500 and 550m, respectively). New Belgium Creek (N.B.) and Anderson Creek were streams at mid elevations (800 and 750m, respectively). Watershed 7 (WS-7) and Watershed 8 (WS-8) were streams at higher elevations (950 and 1000m, respectively). WS-1, N.B., and WS-7 flowed through basins with 20-40 year old vegetation while WS-2, Anderson, and WS-8 flowed through basins with 450+ year old vegetation. Basin size ranged from 12.4 (WS-7) to 97.8ha (WS-1) (Table 2.1). Stream reaches (50m long) were located upstream

of stream gauges or access roads except for WS-2 which was located below the stream gauge. See chapter 2 for riparian characterizations of study sites.

Macroinvertebrate collections and laboratory procedures

Benthic macroinvertebrate samples were collected each season beginning June 2003 through May 2004 (Table 3.1). Summer benthic samples were collected in late June before stream flow was too low to collect samples. Autumn samples were collected in late November after stream flow returned to levels high enough to provide flow through the sampling net. Winter and spring samples were collected during periods of relatively stable stream flow, avoiding rain events (early March and May, respectively). Emergence samples were collected multiple times beginning in June 2003 and extending through June 2004 (Table 3.1); emergence traps were set for 6-8 days per sampling period (Table 3.1).

Six benthic samples and four emergence samples were collected in each 50m study reach each sampling period. Benthic sample locations were randomized each sampling period but emergence sample locations were randomized once at the onset of sampling. Benthic invertebrates were collected with a 0.25mm mesh Surber sampler (0.093 m^2) only in riffle/cascade stream units on gravel and cobble substrates. Emergence samplers consisted of pvc frames covering 0.25 m^2 stream bed draped with 0.60mm mesh nets. A small amount of unscented, biodegradable soap was added to the water in emergence trap collecting cups to decrease surface tension; in cold weather, rock salt was

added to serve as both an antifreezing and preservative agent. All samples were stored in 95% ethanol.

Benthic and emergent insects were identified to genus when possible (Brown 1972, McAlpine et al. 1981, Stewart and Stark 1993, Merritt and Cummins 1996, Wiggins 1996). Individuals of the family Chironomidae were identified to sub-family or tribe in benthic samples, and family level in emergence samples. Non-insects were typically identified to order (Thorp and Covich 1991). Young-instar insects and individuals damaged during sampling or storage were identified to the lowest taxonomic resolution possible, typically order or family. All individuals in each sample were identified, and functional feeding groups as well as habit trait groups were assigned to benthic macroinvertebrates when possible (Merritt and Cummins 1996, Wiggins 1996). Since physical variables were measured to represent stream reaches, individual benthic samples were pooled to represent each stream reach; proportions of functional feeding groups and habit trait groups were calculated on these pooled data. Patterns in cumulative adult insect emergence were compared to cumulative degree-days in gauged streams. Cumulative emergence was based on emergence rates (No. individuals m^{-2} day^{-1}) from each collection period. Cumulative emergence was the running sum of these values.

Instream characterizations

Instream attributes were characterized each season beginning June 2003. Six transects were established perpendicular to stream flow at every 10m along

stream reaches (including 0m as the first transect). Wetted stream widths were measured at these transects; stream widths were used to represent stream size. Substrate type was characterized at 11 points across each transect (0%, 10%, 20%, ….100% of stream width) by size as silt, sand, gravel, cobble, boulder, bedrock, small wood (<10cm diameter), or large wood (>10cm diameter) (modified from Wolman 1954). Mean substrate composition (%) was calculated each season by pooling individual transects within each site for a reach estimate. Fine substrates were defined as the combination of silt and sand. Coarse substrates were defined as the combination of cobble, boulder, bedrock, and large wood. Retentive substrates were defined as the combination of boulder, large wood and small wood.

Allochthonous litterfall

Allochthonous litterfall was collected continuously between July 2003 and October 2003. Litter traps consisted of circular laundry baskets (0.125 m^2) with 0.6mm mesh nets. To characterize major patterns in litterfall, six litter traps per stream were located under dominant overstory and understory vegetation; dominant riparian species were assessed visually. Leaf litter was collected monthly, dried at 60 ºC for 24-36 hours, and weighed.

Stream discharge and water temperature

Mean daily stream discharge and water temperature data were obtained from the H.J. Andrews Experimental Forest website (www.fsl.orst.edu/lter).

These data were only available for gauged streams (WS-1, WS-2, WS-7, and WS-8). Discharge data presented are daily averages from the 14-day period prior to sampling at each stream. Estimates of stream discharge for N.B. and Anderson were calculated by standardizing discharge values per unit area from gauged basins and applying these averages to the basin areas of N.B. and Anderson. Cumulative stream temperature was calculated as the cumulative mean daily water temperature in each gauged stream beginning January 1st through December 31st, 2003 and also beginning January 1st through June 30th, 2004. Water temperature was not available for N.B. and Anderson.

Statistical analyses

Relationships between benthic functional feeding group and habit trait group proportions and local stream conditions were tested using linear regression (Microsoft Excel). All regressions included data from each stream each season with one exception. Because litterfall was only collected in summer and autumn, regressions with benthic proportions and litterfall were only calculated for summer and autumn.

Table 3.1 Complete benthic and emergence sample collection periods from June 2003 to June 2004.

season	benthic	emergence
summer 2003	June 19-24	June 24-30 July 10-16 July 24-30 August 7-13 August 22-28
autumn 2003	Nov. 30 - Dec. 1	Sept. 25 - Oct. 2 November 7-14
winter 2004	March 5-6	December 23-31 March 6-13
spring 2004	Apr. 30 - May 1	April 4-11 May 2-9 May 23-31
summer 2004		June 24-30

RESULTS

Study stream attributes

Stream widths were generally greater at the low elevation streams but within individual streams, stream widths increased associated with changes in stream discharge (Table 3.2). Stream discharge was lowest in summer and highest in winter in all streams (Table 3.2). Percent fine substrates were highly variable but were generally highest in one high elevation stream (WS-7). Percent coarse substrates were generally lower in both high elevation streams. Percent retentive substrates were variable among streams and were primarily influenced by abundance of boulders, but in one high elevation stream (WS-8), both small and large wood were proportionally more abundant than in other streams (Table 3.2). Allochthonous litterfall (mg m^{-2} day^{-1}) was 3 to 30 times higher in autumn than in summer (Table 3.2).

Functional feeding group and habit trait group proportions

In classifications by functional feeding groups, benthic macroinvertebrate communities were dominated by the collector gatherers (Table 3.3) while shredders comprised on average 14.8% and scrapers comprised on average only 8.0% of total macroinvertebrate densities. Percent shredders were negatively correlated with stream widths (Table 3.4, Fig. 3.1), but they were not correlated with percent retentive substrates or allochthonous litterfall (Table 3.4). In contrast, percent scrapers were positively correlated with stream size (Table 3.4, Fig. 3.2).

Table 3.2 Study reach attributes of headwater streams in the H.J. Andrews Experimental Forest.

	WS-1	WS-2	N.B.	Anderson	WS-7	WS-8
Stream width (m)						
summer	1.9	2.1	1.2	1.9	1.2	1.1
autumn	2.3	3.0	1.8	2.4	1.6	1.6
winter	2.8	2.5	2.3	2.7	1.6	1.9
spring	2.0	2.3	2.1	2.4	1.3	1.8
Fine substrates (%)						
summer	18.2	6.1	13.6	10.6	31.8	7.6
autumn	13.6	0.0	18.2	7.6	30.3	13.6
winter	4.5	4.5	16.7	16.7	10.6	21.2
spring	19.7	6.1	15.2	21.2	25.8	30.3
Coarse substrates (%)						
summer	50.0	42.4	51.5	53.0	28.8	30.3
autumn	37.9	34.8	34.8	48.5	33.3	27.3
winter	47.0	31.8	39.4	42.4	15.2	33.3
spring	53.0	50.0	48.5	43.9	13.6	25.8
Retentive substrates (%)						
summer	9.1	16.7	7.6	15.2	6.1	13.6
autumn	3.0	9.1	16.7	7.6	16.7	21.2
winter	10.6	10.6	6.1	6.1	3.0	22.7
spring	19.7	21.2	9.1	9.1	3.0	13.6
Litterfall (mg m^{-2} day^{-1})						
summer	0.4	0.6	0.3	0.9	0.2	0.3
autumn	5.3	1.8	8.9	3.0	2.6	2.6
Stream discharge (l s^{-1})						
summer	4.7	4.8	3.4	3.1	0.8	1.2
autumn	47.7	24.4	19.6	17.9	2.4	5.5
winter	56.7	32.0	32.1	29.3	7.1	10.1
spring	40.2	23.7	22.8	20.8	4.8	7.2

Table 3.3 Benthic functional feeding group proportions in headwater stream reaches.

	WS-1	WS-2	N.B.	Anderson	WS-7	WS-8
collector filterers (%)						
summer	1.2	0.6	1.6	0.6	3.9	0.9
autumn	30.2	0.6	2.2	0.9	2.7	2.1
winter	2.3	1.1	3.1	2.3	4.5	15.4
spring	4.5	0.2	0.8	1.9	0.2	1.7
collector gatherers (%)						
summer	61.1	39.9	38.3	56.5	47.5	56.5
autumn	25.2	32.3	39.7	53.4	42.7	50.3
winter	58.7	37.9	58.6	60.2	33.1	35.6
spring	50.7	48.9	38.6	51.7	37.3	42.6
predators (%)						
summer	14.1	20.2	13.6	21.7	8.3	15.3
autumn	11.2	16.3	20.9	12.0	16.5	16.9
winter	8.9	13.6	11.2	11.4	11.1	12.8
spring	10.7	13.9	18.2	16.9	12.3	17.1
scrapers (%)						
summer	3.2	9.2	10.0	3.5	6.4	2.0
autumn	3.8	19.4	8.5	13.4	13.1	3.0
winter	5.5	16.3	9.6	11.7	12.5	5.0
spring	1.7	10.9	4.8	7.8	5.6	4.1
shredders (%)						
summer	12.1	16.0	26.9	10.2	22.2	9.8
autumn	18.0	17.8	15.5	11.1	16.5	13.1
winter	16.7	13.2	6.8	6.6	19.0	18.0
spring	16.2	13.2	12.5	10.2	17.8	16.4
pupae, parasites, unknown (%)						
summer	8.3	14.1	9.7	7.5	11.7	15.5
autumn	11.6	13.7	13.2	9.2	8.5	14.6
winter	7.9	17.9	10.7	7.8	19.9	13.2
spring	16.2	12.9	25.1	11.5	26.7	18.1

Table 3.4 Regression summary statistics for relationships between functional feeding group and habit trait group proportions and local stream attributes. Relationships between stream attributes were also included.

Regression Equation	r^2	F stat.	p value
SHREDDERS			
% shredders = -3.6(stream width) + 22.0	0.16	4.18	0.05
% shredders = -0.1(% retentive substrates) + 15.5	0.01	0.12	0.73
% shredders = -0.1(litterfall) + 16.0	<0.01	0.04	0.85
SCRAPERS			
% scrapers = 4.1(stream width) - 0.1	0.20	5.44	0.03
CLINGERS			
% clingers = 0.4(% coarse substrates) + 30.3	0.19	5.12	0.03
% clingers = 0.4(stream discharge) + 37.3	0.40	14.91	<0.01
SPRAWLERS			
% sprawlers = -0.2(stream discharge) + 25.2	0.24	6.89	0.02
% sprawlers = 0.2(% fine substrates) + 18.2	0.06	1.30	0.27
BURROWERS			
% burrowers = -0.1(% fine substrates) + 9.6	0.03	0.68	0.42
% burrowers = (< -0.1)(stream discharge) + 8.8	0.01	0.22	0.64
PHYSICAL ATTRIBUTES			
% fine substrates = -0.2(stream discharge) + 18.5	0.12	3.04	0.10
% retentive substrates = -0.1(stream discharge) + 12.5	0.02	0.44	0.51
% coarse substrates = -0.2(stream discharge) + 34.0	0.11	2.77	0.11
stream width = (< 0.1)(stream discharge) + 1.6	0.54	25.9	<0.01
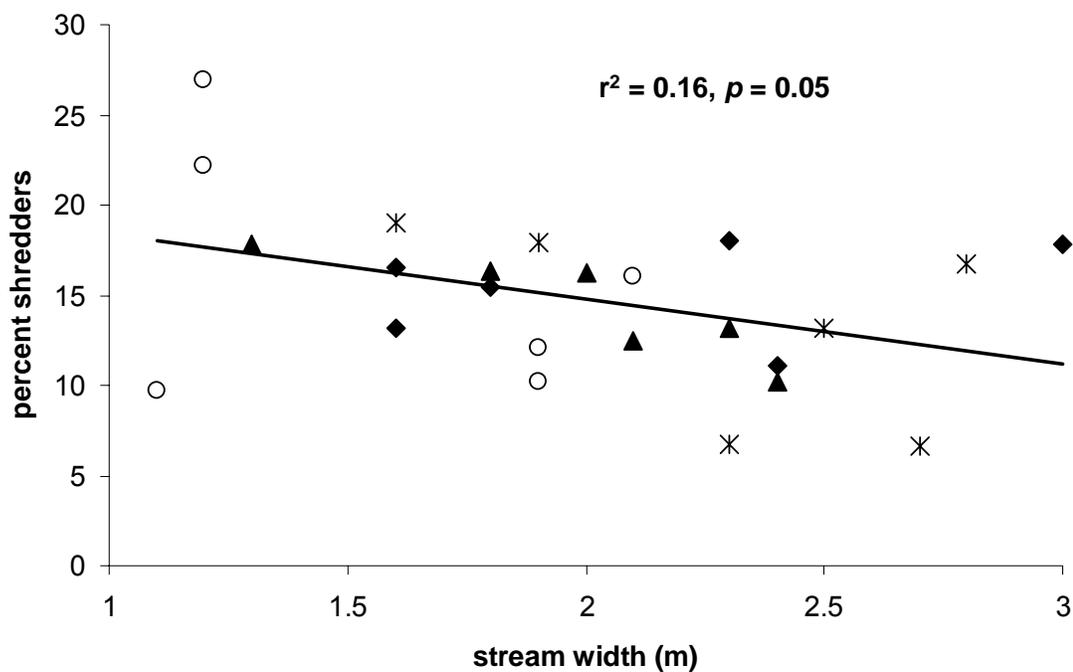
Fig. 3.1 Relationship between percent shredders and stream width. Symbols correspond to season when sample was collected: ○ = summer, ♦ = autumn, ✶= winter, ▲ = spring.
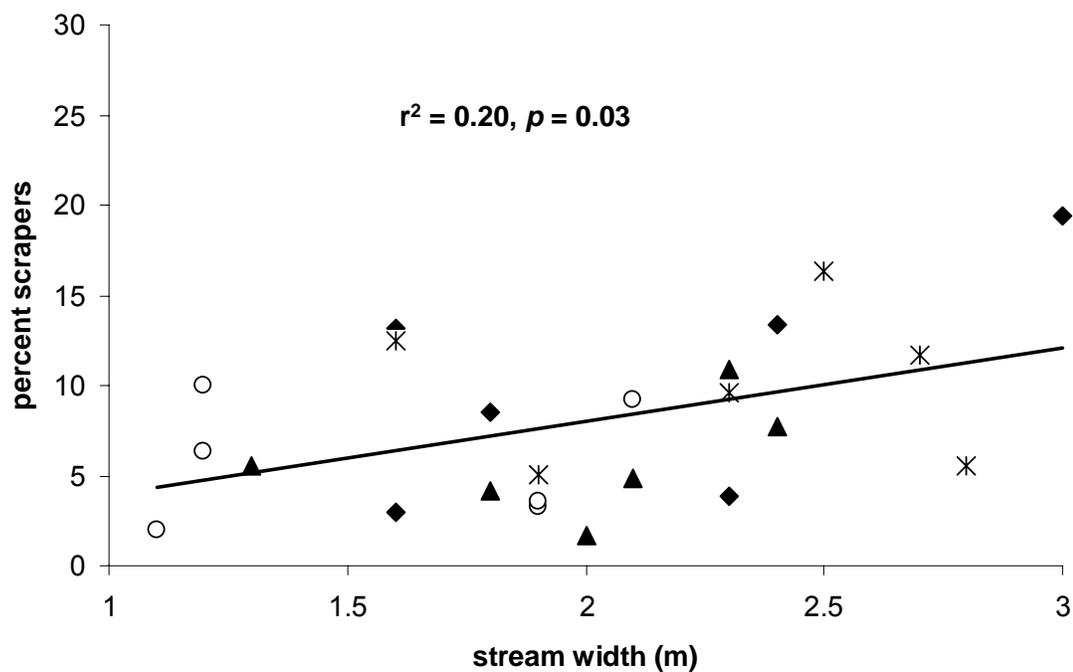
Fig. 3.2 Relationship between percent scrapers and stream width. Symbols correspond to season when sample was collected: ○ = summer, ♦ = autumn, ✶= winter, ▲ = spring.

When benthic macroinvertebrates were grouped by habit-traits, communities were dominated by clingers (Table 3.5). Sprawlers comprised on average 21.2% and burrowers comprised only 8.3% of total macroinvertebrate densities. Percent clingers were positively correlated with both percent coarse substrates and stream discharge (Table 3.4, Fig. 3.3 and 3.4, respectively). Percent sprawlers were negatively correlated with stream discharge (Table 3.4, Fig. 3.5) but were not significantly correlated with percent fine substrates. Percent burrowers were not significantly correlated with percent fine substrates or stream discharge (Table 3.4).

Adult insect emergence

Emergence in low and mid elevation streams generally followed a mid spring to mid summer pattern with multiple peaks in emergence (Fig. 3.6). High elevation streams generally followed a unimodal pattern in early summer, but in June 2004, emergence at high elevation streams had not yet reached values similar to the prior year (Fig. 3.6). Peaks in emergence during summer months were represented by numerous taxa; emergent insect taxa richness was generally highest in summer (see Chapter 2).

The most abundant taxa nearly every collection period were midges (Chironomidae sp. and Chironomidae/Ceratopogonidae sp.,) (Fig 3.7 and 3.8, Appendix V). However, several other taxa emerged in substantial numbers throughout the year. Abundant taxa during early to mid summer were the mayfly *Paraleptophlebia* (Leptophlebiidae: Ephemeroptera), the caddisfly *Dolophilodes*

Table 3.5 Benthic habit trait group proportions in headwater stream reaches.

	WS-1	WS-2	N.B.	Anderson	WS-7	WS-8
burrowers (%)						
summer	4.6	3.4	10.5	10.5	2.1	5.8
autumn	5.9	8.7	10.6	22.8	10.2	18.5
winter	4.2	8.0	9.5	8.2	9.1	4.2
spring	6.7	5.2	8.1	8.5	6.8	6.5
climbers (%)						
summer	0.7	1.7	0.2	1.7	0.1	0.1
autumn	0.0	1.0	0.4	1.3	0.1	0.1
winter	0.1	1.2	0.0	0.6	0.1	0.5
spring	0.4	0.8	0.1	1.0	0.0	0.2
clingers (%)						
summer	38.8	50.5	41.5	40.4	29.1	25.0
autumn	50.0	43.3	38.0	43.9	32.4	30.1
winter	52.4	51.8	52.1	48.0	43.1	58.4
spring	51.2	48.7	57.7	51.4	35.6	37.4
sprawlers (%)						
summer	23.6	18.4	29.5	20.5	38.5	31.5
autumn	23.4	23.8	27.3	14.7	27.8	20.3
winter	17.1	15.6	8.2	9.2	27.1	16.3
spring	20.5	22.7	14.2	11.3	26.2	21.2
swimmers (%)						
summer	9.4	16.0	8.1	12.4	14.3	20.1
autumn	10.6	15.0	9.5	9.6	16.0	14.8
winter	22.3	16.7	28.3	29.1	13.8	14.7
spring	13.7	16.8	11.1	19.3	19.1	20.5
unknown (%)						
summer	22.9	9.9	10.3	14.6	15.9	17.4
autumn	10.0	8.2	14.2	7.8	13.5	16.2
winter	3.9	6.7	1.8	4.8	6.8	5.9
spring	7.6	5.8	8.9	8.5	12.2	14.2
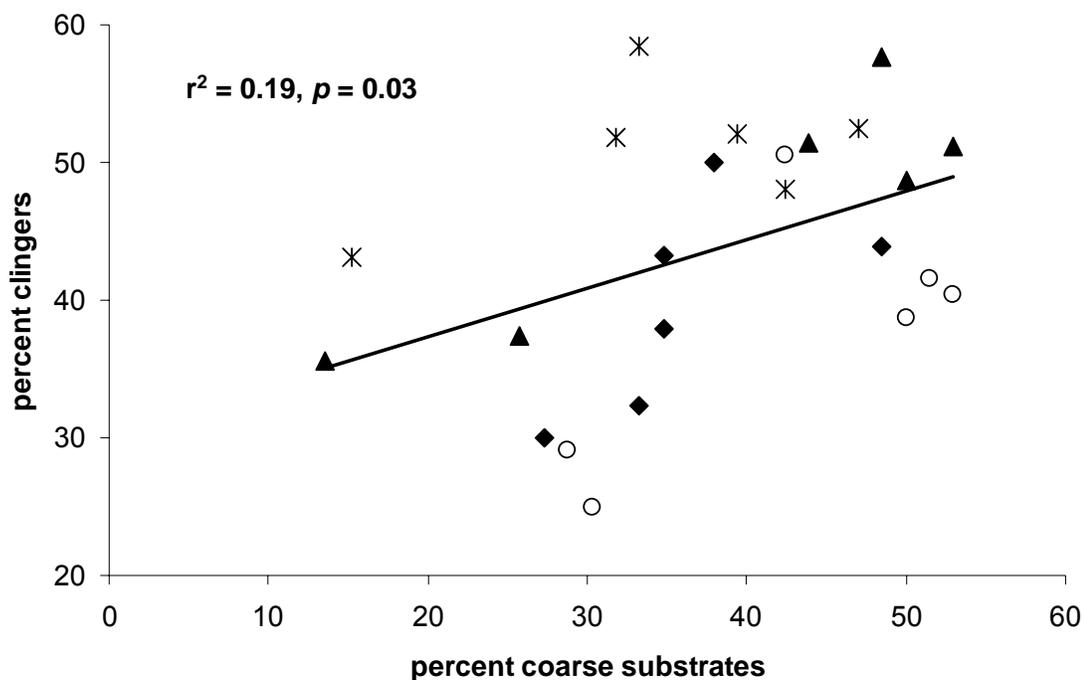
Fig. 3.3 Relationship between percent clingers and percent coarse substrates. Symbols correspond to season when sample was collected: ○ = summer, ◆ = autumn, ✳ = winter, ▲ = spring.
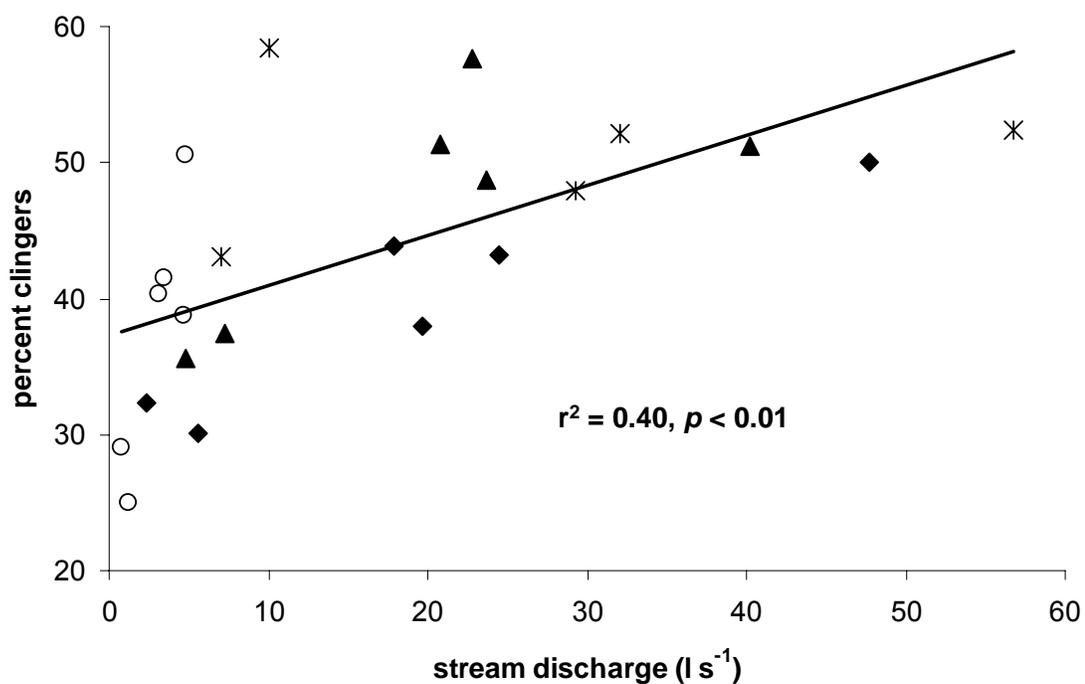
Fig. 3.4 Relationship between percent clingers and stream discharge. Symbols correspond to season when sample was collected: ○ = summer, ◆ = autumn, ✳ = winter, ▲ = spring.
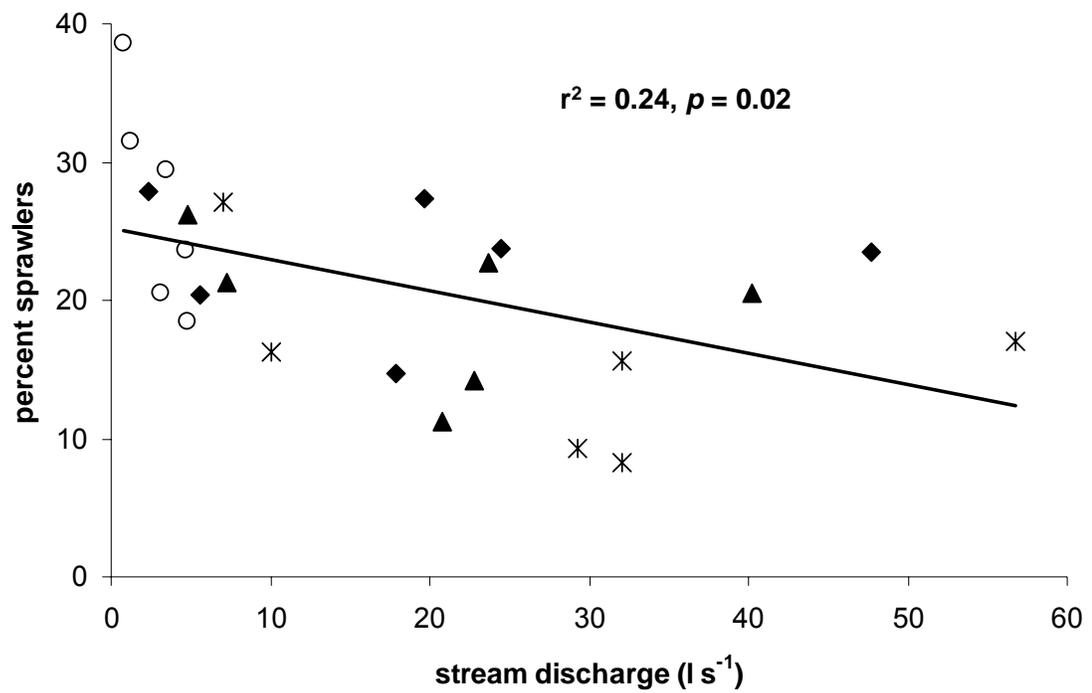
Fig. 3.5 Relationship between percent sprawlers and stream discharge. Symbols correspond to season when sample was collected: ○ = summer, ◆ = autumn, ✳ = winter, ▲ = spring.
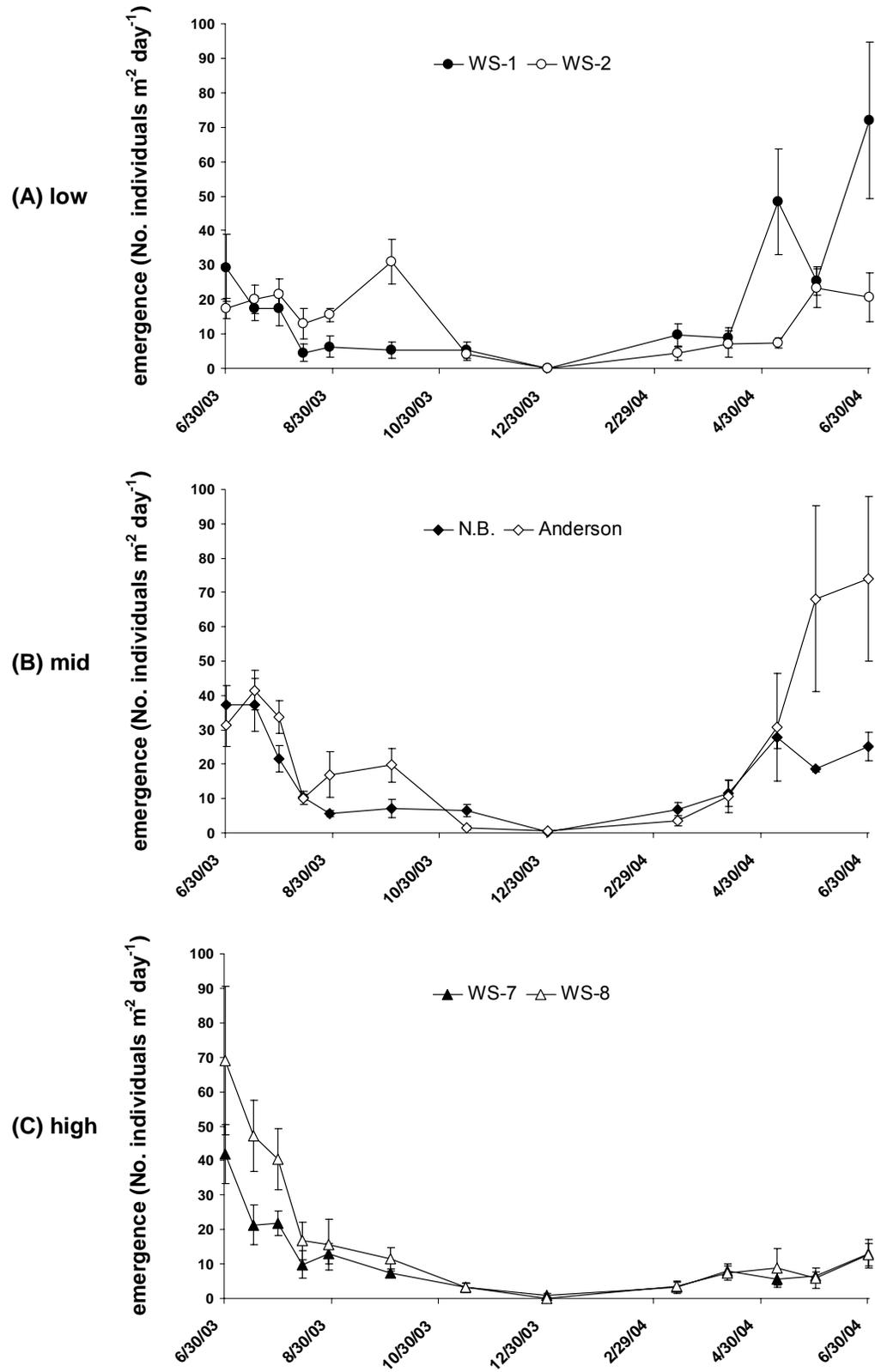
Fig. 3.6 Mean (± 1SE) community emergence of adult insects in (A) low, (B) mid, and (C) high elevation streams from June 2003 to June 2004.
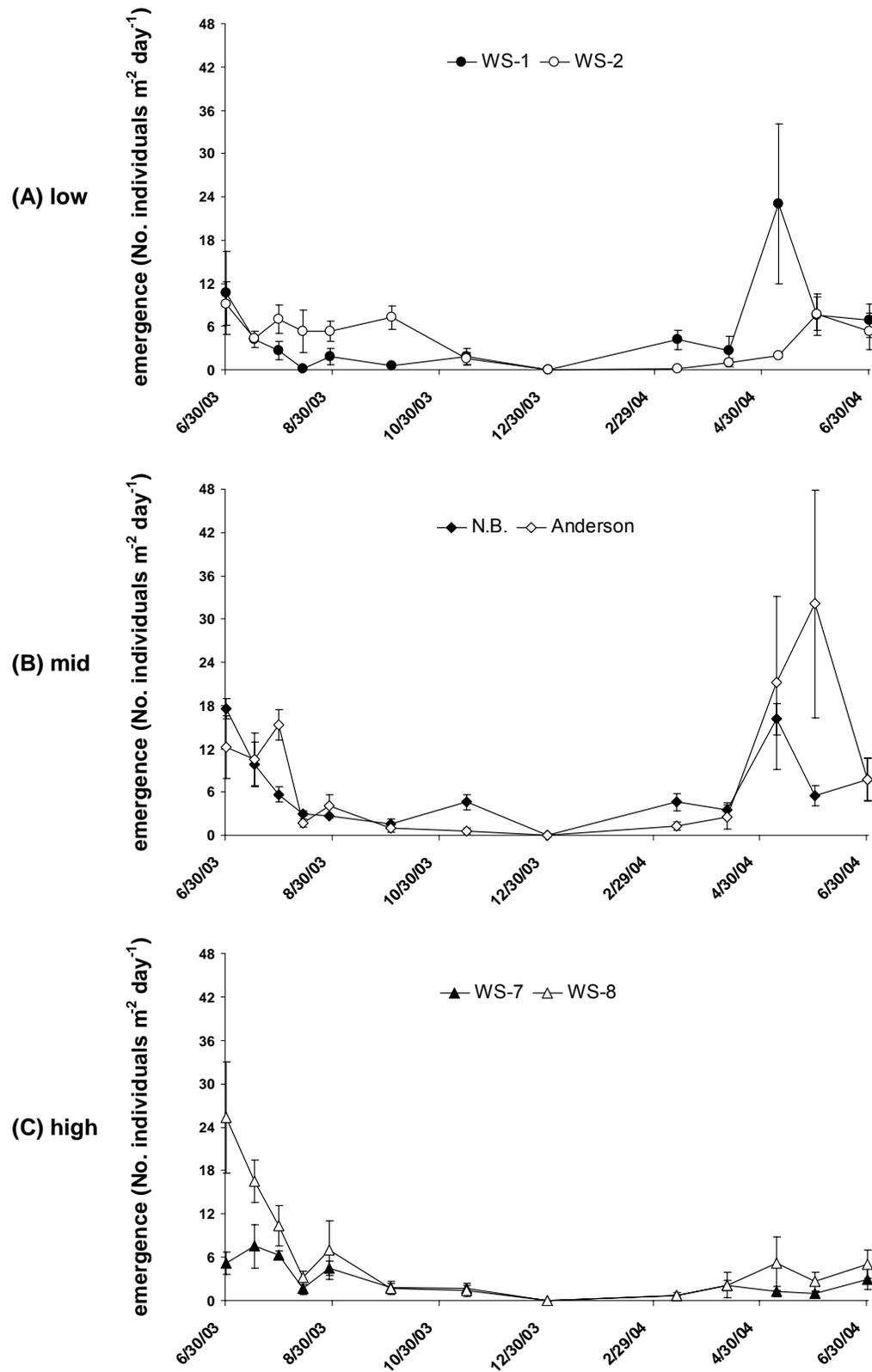
Fig. 3.7 Mean (± 1SE) emergence of adult midges (Chironomidae: Diptera) in (A) low, (B) mid, and (C) high elevation streams from June 2003 to June 2004.
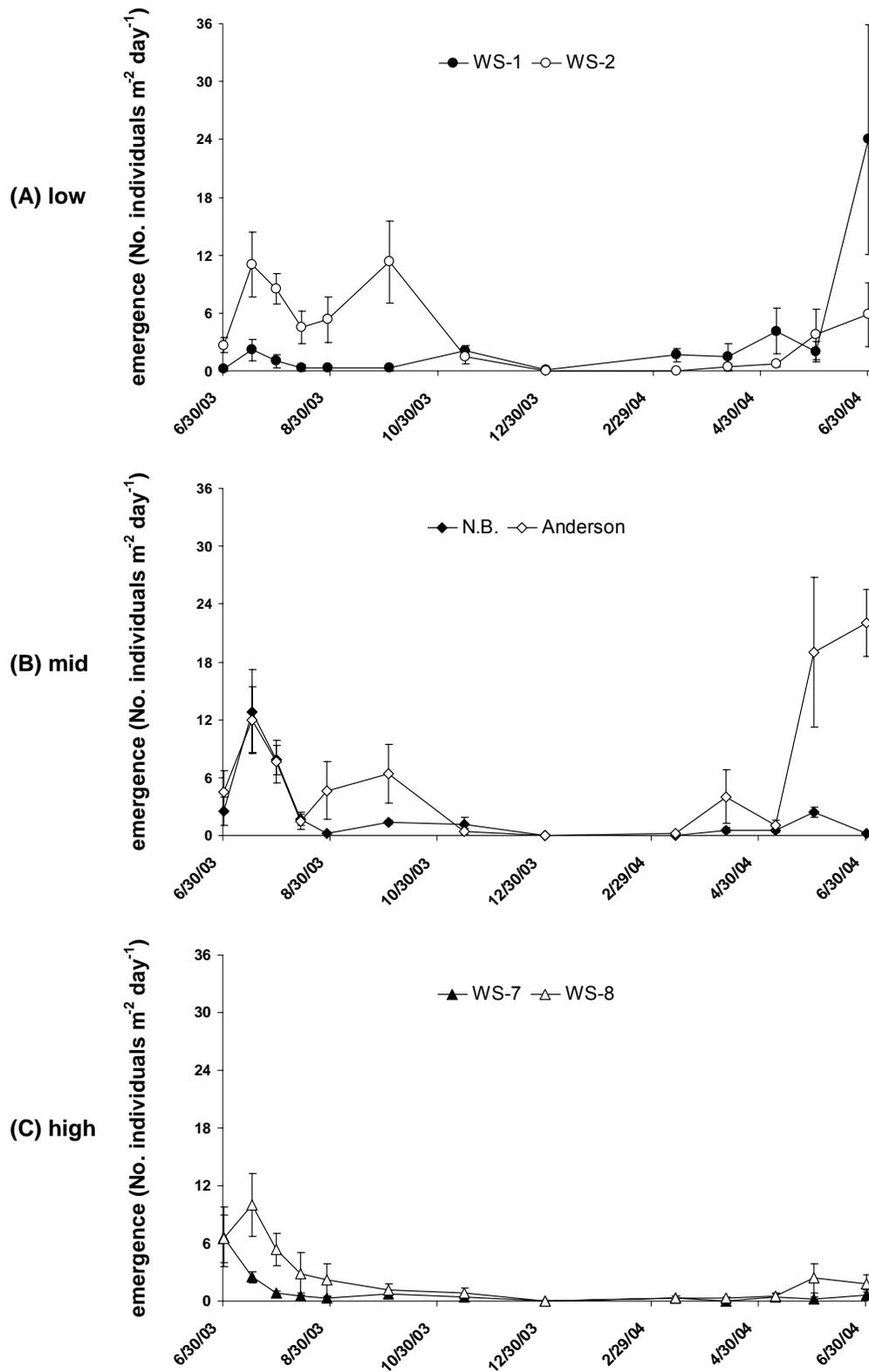
Fig. 3.8 Mean (± 1SE) emergence of adult midges/biting midges (Chironomidae/Ceratopogonidae: Diptera) in (A) low, (B) mid, and (C) high elevation streams from June 2003 to June 2004.

(Philopotamidae: Trichoptera), and two stonefly genera, *Alloperla/Bisancora* (Chloroperlidae: Plecoptera), and *Malenka* (Nemouridae: Plecoptera). In autumn, the stonefly *Despaxia* (Leuctridae: Plecoptera), and the dancefly *Clinocera* (Empididae: Diptera) were commonly collected (Appendix V). Very few taxa emerged in late December, but an apterous stonefly *Paracapnia disala* (Capniidae: Plecoptera) was collected at one mid and two high elevations streams (Appendix V). In spring, many taxa emerged at various rates among streams, but besides midges, *Alloperla/Bisancora* was collected frequently (Appendix V).

During the six month period before sampling began in June 2003, cumulative water temperature in both low elevation streams reached levels between 200 and nearly 400 degree-days higher than in either high elevation stream (Fig. 3.9A). However, from late June through December 2003, cumulative community emergence was highest in one high elevation stream (WS-8) (Fig. 3.9B). Between January 1st and May 9th, 2004, cumulative water temperature increased to levels between 100 and 250 degree-days higher in both low elevation streams than either high elevation stream (Fig. 3.10A). In early May, several trends in cumulative community emergence began to develop. Cumulative emergence was higher in one low elevation (WS-1) and one mid elevation stream (Anderson) than other streams (Fig. 3.10B). By June 30th, cumulative community emergence in these two streams (WS-1 and Anderson) was two to three times greater than in the other streams at low and mid elevations (WS-2 and N.B.) (Fig. 310B). During spring 2004, cumulative

community emergence at both high elevation streams remained very low (Fig.

3.10B). Twelve univoltine taxa (12.6% of the total number of emergent taxa

collected from June 2003 to June 2004), were collected earlier in at least one low

elevation stream than either high elevation stream (Table 3.6).
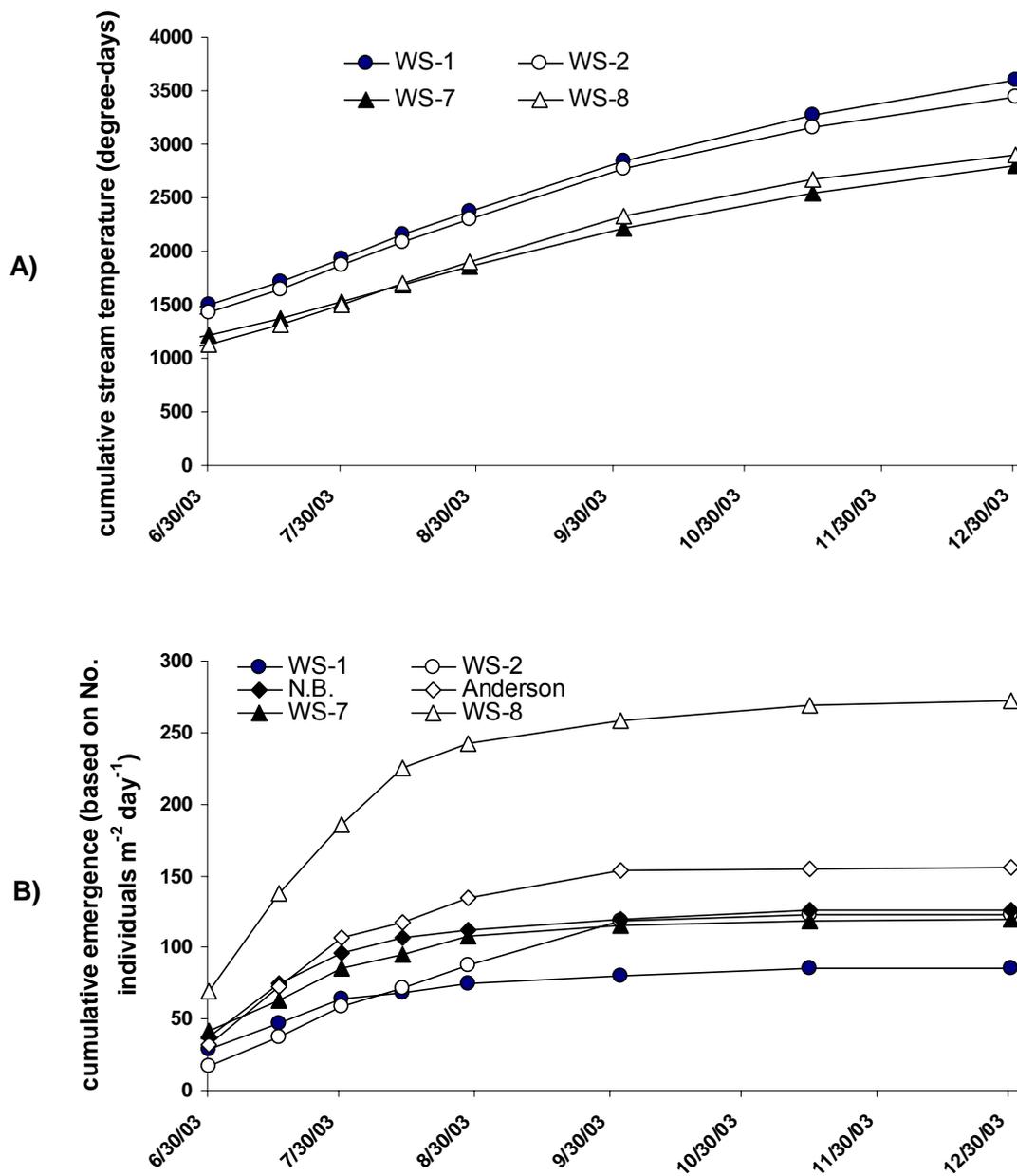
Fig. 3.9 Relationships between A) total cumulative water temperature (degree-days) and B) mean total community emergence of adult insects from June to December 2003.
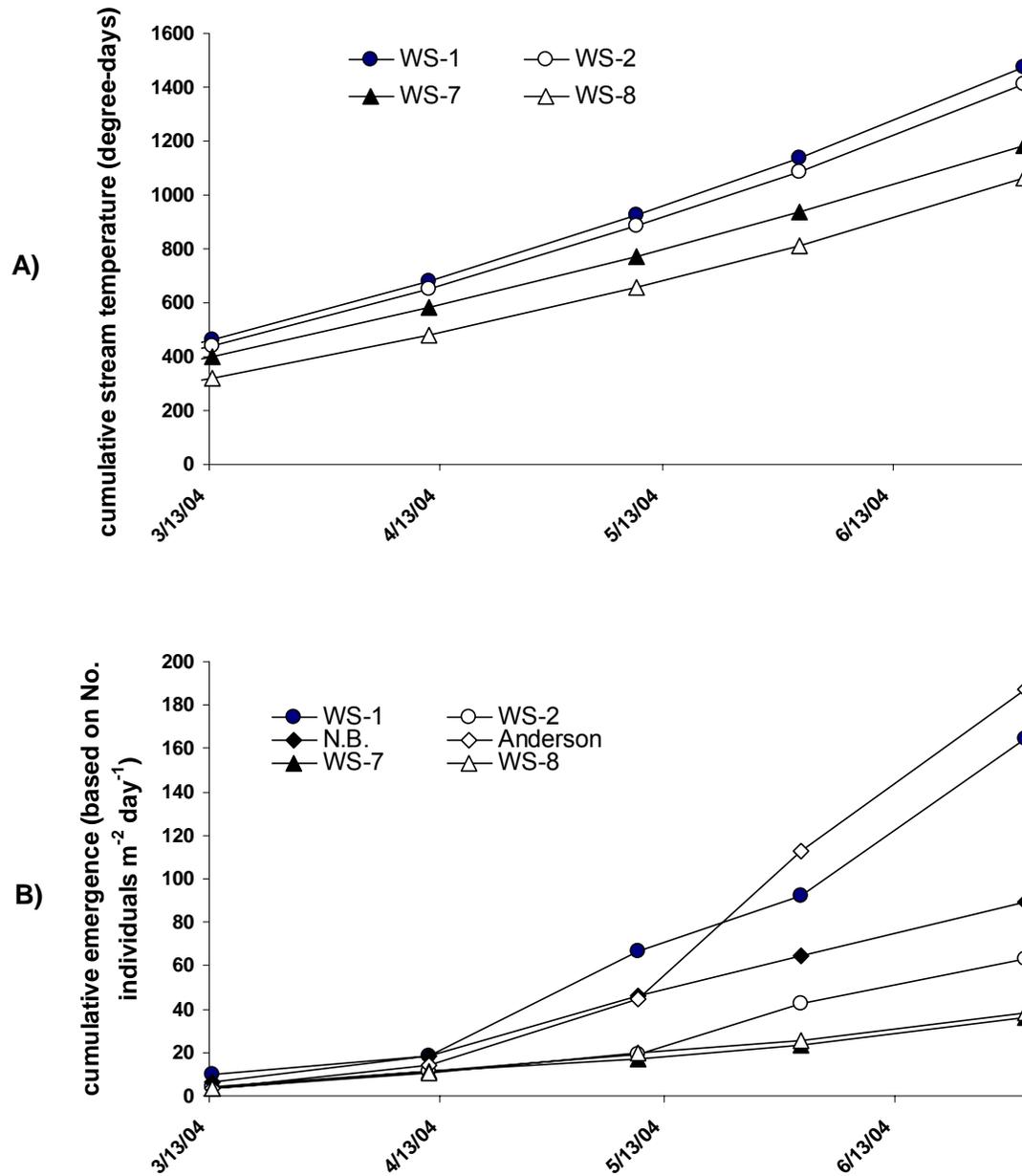
Fig. 3.10 Relationships between A) total cumulative water temperature (degree-days) and B) mean total community emergence of adult insects from March to June 2004.

Table 3.6 List of univoltine taxa which emerged earlier in at least one lower elevation stream than either higher elevation stream. Only taxa with univoltine life cycles (one generation per year) and those that were represented by at least 10 individuals were included in this list. Date of earliest capture was inferred from collections made in both 2003 and 2004. These taxa represent 12.6% of the total number of emergent taxa collected at all streams throughout the collecting year.

ORDER	FAMILY	GENUS	WS-1	WS-2	N.B.	Anderson	WS-7	WS-8
Diptera	Empididae	*Clinocera*	13-Mar-04	11-Apr-04	13-Mar-04	13-Mar-04	11-Apr-04	11-Apr-04
		Neoplasta		30-Jun-04	30-Jun-04	30-Jun-03	16-Jul-03	
	Simuliidae	*Prosimulium*	13-Mar-04		9-May-04	9-May-04	30-Jun-04	30-Jun-03
	Tipulidae	*Pedicia*	13-Mar-04	13-Mar-04	11-Apr-04	11-Apr-04	9-May-04	9-May-04
Ephemeroptera	Ameletidae	*Ameletus*	9-May-04	31-May-04	31-May-04	31-May-04	30-Jul-03	
	Heptageniidae	*Cinygma*	13-Mar-04	30-Jun-04	30-Jun-04	30-Jun-04	30-Jun-04	30-Jun-04
		Ironodes	11-Apr-04	9-May-04	9-May-04	9-May-04	9-May-04	
Plecoptera	Chloroperlidae	*Alloperla/Bisancora*	11-Apr-04	31-May-04	31-May-04	31-May-04	31-May-04	31-May-04
	Nemouridae	*Ostrocerca*	11-Apr-04	11-Apr-04		9-May-04	30-Jun-03	30-Jun-03
	Peltoperlidae	*Yoraperla*	9-May-04	9-May-04	31-May-04	31-May-04	31-May-04	30-Jun-04
Trichoptera	Brachycentridae	*Micrasema*		11-Apr-05		30-Jul-03	30-Jun-04	30-Jun-03
	Glossosomatidae	*Anagapetus*		9-May-04	31-May-04		31-May-04	

DISCUSSION

As suggested by stream ecosystem theory (Vannote et al. 1980, Minshall et al. 1983, Grubaugh et al. 1996), functional composition was related to stream size in these headwater streams. Habit-trait composition however, was related to stream substrate composition or stream discharge. Though there was evidence for adult insects emerging earlier in spring in one stream where cumulative water temperature was higher, total community emergence among streams was highly variable and influenced by pulses in emergence that coincided with particular sampling periods.

Benthic shredders are thought to comprise large proportions of macroinvertebrate communities in headwater streams (Vannote et al. 1980), but results from this study suggest they comprise at most 25 percent of overall macroinvertebrate densities. Previous studies of headwater streams in H.J. Andrews (Hawkins and Sedell 1981, Minshall et al. 1983) found shredders in greater proportions than this study, but in one of these studies, midges were excluded from analyses yet they often comprise a large proportion of total benthic densities. Other studies of headwater streams have found similar, or lower proportions of shredders than in this study (Grubaugh et al. 1986, Price et al. 2003, Hernandez et al. 2005). Nevertheless, this study found that shredders decreased proportionally with increasing stream width.

Along stream continua, macroinvertebrates that feed primarily on algae and biofilms often increase proportionally in larger downstream reaches (Hawkins and Sedell 1981, Minshall et al. 1983, Grubaugh et al. 1986). Even

though benthic scrapers comprised low proportions of total benthic densities in this study, scraper proportions increased with increasing stream width; however, these results were influenced by a genus of snails, *Juga* (*Pleuroceridae*: Prosobranchia), which were collected in higher densities in WS-2 than other streams. In fact, they were only collected in WS-1 and WS-2, and are typically restricted to lower elevations (Hawkins and Furnish 1987). The differences in abundance of *Juga* between WS-1 and WS-2 are difficult to understand because *Juga* are generally more numerous in streams with finer substrates (Hawkins and Furnish 1987); percent fines were higher in WS-1 than WS-2.

Because these snails are generalist feeders and may destroy fixed retreats of sessile stream organisms, densities of other benthic macroinvertebrates may be adversely affected (Hawkins and Furnish 1987). These snails are long-lived, and macroinvertebrate densities may be consistently lower in streams where they are present. Compared to other streams in this study, total benthic macroinvertebrate densities were lowest in WS-2 where *Juga* were most abundant, each season except autumn.

Proportions of scrapers were higher in most streams during both autumn and winter than in either summer or spring. However, proportions of scrapers were not higher in streams with lower canopy cover. Seasonal trends in proportions of scrapers followed life-cycle patterns of several winter-growing scrapers including *Ironodes* (Heptageniidae: Ephemeroptera), *Cinygmula* (Heptageniidae: Ephemeroptera), and *Anagapetus* (Glossosomatidae:

Trichoptera) which were collected in higher densities in autumn and winter than summer and spring.

Though functional feeding composition of macroinvertebrate communities described possible relationships with food resource availability from smaller to larger streams, investigations of habit trait composition suggested that macroinvertebrates respond to differences among streams in microhabitat availability. Patterns in habit trait composition also reflected seasonal changes in stream attributes. Clinger proportions were generally higher in streams with higher proportions of coarse substrates and during periods of greater stream discharge, suggesting a shift in macroinvertebrate communities towards taxa adapted for increased stream flow velocities.

Proportions of benthic sprawlers were correlated with stream discharge but not proportions of fine substrates. Because benthic sprawlers inhabit the surfaces of fine sediments or organic matter accumulations, higher stream discharge in all streams may have displaced some of these individuals. In these high gradient streams where discharge is flashy in late autumn through spring, discharge may be a more critical limiting factor than substrate availability.

Benthic burrowers did not increase proportionally with fine substrates as originally expected. Percent burrowers were fairly similar among streams regardless of the relative abundance of fine substrates. Some burrowing macroinvertebrates inhabit fine sediments while others burrow into organic matter accumulations. Because small streams in the Central Cascade Range of

Oregon are highly retentive (Speaker et al. 1984), availability of organic matter microhabitats may be greater than that of fine substrates in these headwaters.

Trends in emergence among headwater streams suggested high variability in overall numbers and in cumulative emergence over time among streams of different sizes. Emergence in one very small stream (WS-8) was much higher than all other streams from early summer to mid summer 2003. Because of much higher emergence rates during this period, cumulative emergence in this stream remained higher in 2003. The following spring, patterns in emergence among streams demonstrated more insects emerging in one low (WS-1) and one mid elevation (Anderson) stream than other streams. Results from this study suggest that peaks in total community emergence may occur earlier (in spring) in larger headwater streams at lower elevations. Though peaks in emergence may occur later in the year in very small headwater streams, total cumulative emergence may exceed that in larger streams. Results from this study indicate that relationships between stream water temperature and total cumulative emergence are not clear. Though cumulative stream water temperature was very similar between years, total community emergence was very different in four of these headwater streams between 2003 and 2004.

Differences in functional feeding and habit trait groups and emergence patterns among headwater streams within a relatively small landscape (6400 ha) helped explain the roles of microhabitat factors in community composition. Sampling benthic macroinvertebrates seasonally increased variability for physical stream attributes which helped to explain trends in community composition.

These results suggest microhabitat characterization in headwater streams in combination with life-history trait analyses is important in understanding patterns in macroinvertebrate community composition. This study also documented high variability in emergence rates among streams likely influenced by behavioral responses of emerging insects to changes in environmental conditions. Emergence pulses varied among streams from lower to higher elevations which coincided with specific sampling periods.

CHAPTER 4: Summary

This study compared headwater macroinvertebrate communities between streams through deciduous dominated riparian zones with paired streams through old growth conifer riparian zones. Paired-stream analyses removed variation among streams at different elevations in order to concentrate on differences related to riparian vegetation. Results from this study suggest no long-term residual effects of forest harvest on macroinvertebrate biodiversity or densities in headwater streams of the H.J. Andrews Experimental Forest. Despite similarities among these metrics, multivariate ordination techniques helped elucidate differences in benthic community composition between forest types when red alder was present in riparian zones of previously harvested basins.

Though macroinvertebrate biodiversity and densities were similar between paired streams of different forest types, macroinvertebrate life-history traits varied among headwater streams in relation to stream size, stream substrates, or stream discharge. Patterns in adult insect emergence were highly variable among streams and linkages with cumulative stream water temperature were tenuous. Since physical characteristics of headwater streams often vary with respect to myriad environmental attributes, macroinvertebrate life-history traits helped in understanding organismal response to dynamic environments.

Seasonal sampling of benthic and emergent communities was important in quantifying overall biodiversity as well as patterns in adult emergence. Overall,

131 unique benthic and 89 unique emergent taxa were collected across all streams between June 2003 and June 2004. By sampling seasonally, this study collected 31 benthic and 12 emergent taxa in seasons other than summer. Sixteen taxa were only collected in emergence samples, while 23 taxa were only collected in benthic samples.

Because scientists and land managers have only begun to recognize the importance of headwater streams to larger landscape dynamics and stream network connectivity (Gomi et al. 2002), variation among these streams should be considered in management of these areas. If management plans include conservation components, even the smallest headwaters should be considered because they typically contain unique macroinvertebrate taxa not found in larger streams (see also Dieterich and Anderson 2000, Meyer and Wallace 2001).

Since long-term ecological monitoring is important in understanding temporal coherence with environmental conditions, further studies should examine how headwater macroinvertebrate communities change with continued riparian vegetation succession following forest harvest. Studies involving short-lived species, particularly macroinvertebrates, should include seasonal sampling because these organisms often exhibit adaptations and behaviors related to seasonal conditions. Life-history traits are useful in studies of macroinvertebrate response to natural and anthropogenic environmental alterations because they depict species adaptations to environmental stochasticity.

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APPENDICES

Appendix I Benthic taxa collected in only one stream pooled across seasons. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†). WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

Order	Family	Genus/taxa	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*
Anomopoda	Chydoridae	Chydoridae sp.	+					
Coleoptera	Dytiscidae	Dytiscidae sp. Adult					+	
		Dytiscidae sp. Larvae	+					
	Elmidae	*Heterlimnius*			+			
Decapoda	Astacidae	*Pacifasticus*		+				
Diptera	Empididae	*Hemerodromia*		+				
	Pelecorhynchidae	*Glutops*						+
	Psychodidae	*Maruina*				+		
	Tipulidae	*Antocha*					+	
		Gonomyia						+
		Pedicia						+
		Prionocera					+	
Ephemeroptera	Baetidae	*Acentrella*		+				
	Ephemerellidae	*Caudatella*			+			
		Serratella					+	
Odonata	Cordulegastridae	*Cordulegaster*	+					
Plecoptera	Perlidae	*Doroneuria*			+			
	Perlodidae	*Calliperla*					+	
		Isoperla	+					
		Megarcys			+			
	Pteronarcyidae	*Pteronarcella*	+					
	Taeniopterygidae	*Taenionema*			+			
Trichoptera	Goeridae	*Lepania*					+	
	Hydropsychidae	*Homoplectra*					+	
		Hydropsyche	+					
	Limnephilidae	*Allocosmoecus*				+		
	Limnephilidae	*Chyranda*			+			
	Uenoidae	*Neothremma*			+			
		Oligophleboides			+			
No. of unique taxa			6	3	8	2	7	3
Proportion of total taxa at each stream			7.1	3.7	8.6	2.5	7.9	3.8

Appendix II Emergent taxa collected in only one stream pooled across collection dates. WS-1, N.B., and WS-7 are streams flowing through young growth forests (†). WS-2, Anderson, and WS-8 are streams flowing through old growth forests (*).

Order	Family	Genus/taxa	WS-1[†]	WS-2*	N.B.[†]	Anderson*	WS-7[†]	WS-8*
Coleoptera	Amphizoidae	*Amphizoa*			+			
	Elmidae	*Heterlimnius*			+			
Diptera	Axymiidae	*Axymyia*			+			
	Chaoboridae	*Eucorethra*						+
	Empididae	*Dolichocephala*					+	
		Oreogeton					+	
	Psychodidae	*Maruina*				+		
	Simuliidae	*Parasimulium*						+
	Tipulidae	*Antocha*					+	
		Dicranota			+			
		Elliptera						+
		Erioptera	+					
		Gonomyia				+		
		Limnophila	+					
		Limonia						+
Ephemeroptera	Ephemerellidae	*Ephemerella/Serratella*	+					
Hemiptera	Gerridae	*Gerris*	+					
Plecoptera	Capniidae	*Capnura/Capnia*			+			
	Chloroperldidae	*Kathroperla*						+
	Leuctridae	*Perlomyia*			+			
	Perlodidae	*Chernokrilus*	+					
		Isoperla			+			
	Taeniopterygidae	*Taenionema*			+			
Trichoptera	Calamoceratidae	*Heteroplectron*						+
	Goeridae	*Goeracea*			+			
	Hyroptilidae	Hydroptilidae sp.						+
No. of unique taxa			5	0	9	2	3	7
Proportion of total taxa at each stream			12.5	0	19.1	4.7	7.1	16.7

Appendix III Indicator Species Analyses values for benthic taxa demonstrating differences (p ≤ 0.10) between forest types, or among seasons. Indicator values (% of perfect indication) were derived by combining values of relative abundance and relative frequency (Dufrene and Legendre 1997). Significance of group membership was determined through 1000 Monte Carlo simulations. COL = Coleoptera, COR = Corbiculaceae, CYC = Cyclopoida, DIP = Diptera, EPH = Ephemeroptera, HAR = Harpacticoida, HEM = Hemiptera, HYD = Hydracarina, NEM = Nematoda, ODO = Odonata, OLI = Oligochaeta, PLE = Plecoptera, PRO = Prosobranchia, TRI = Trichoptera. YG = young growth, OG = old growth. Values are listed only for significant differences between forest types, seasons, or both. These 100 taxa represent 54.1% of the total number of taxa evaluated.

			forest type		season			
Order	Family	Genus/taxa	YG	OG	sum	aut	win	spr
COL	Elmidae	Elmidae sp.			34	2	0	22
		*Heterlimnius**	26	0				
		Heterlimnius adult*	7	0				
		Lara			7	21	11	8
		Zaitzevia	8	21				
		Zaitzevia adult			12	0	0	15
	Hydraenidae	*Hydraena*			1	12	1	2
COR	Sphaeriidae	Sphaeriidae sp.	26	5				
CYC	Cyclopoida sp.	Cyclopoida sp.			18	23	1	12
DIP	Blephariceridae	*Agathon*			0	14	16	0
	Ceratopogonidae	*Atrichopogon*			0	17	13	2
		Bezzia/Palpomyia	42	25	24	16	13	13
		Ceratopogoninae sp.			13	34	11	15
	Chironomidae	Chironomidae sp.			40	19	3	13
		Chironomidae pupae			30	3	5	17
		Chironomini	7	0	10	0	0	0
		Orthocladiinae	52	48	28	24	23	25
		Tanypodinae			27	28	12	22
		Tanytarsini			28	25	21	24
	Dixidae	*Dixa*	20	3	23	4	2	0
		Meringodixa			52	1	0	1
		Dixidae sp.			13	1	0	0
	Empididae	*Chelifera*			2	34	4	3
		Clinocera			13	0	0	1
		Empididae sp.			14	11	0	1
		Oreogeton	14	29				
	Psychodidae	*Maruina**	0	8				
		Pericoma/Telmatoscopus			0	9	0	0
		Psychodidae sp.*			8	0	0	0
	Simuliidae	*Prosimulium*			2	0	41	12
		Simuliidae sp.	42	15	5	34	22	3
		Simulium	19	1	0	10	17	0
	Thaumaleidae	*Thaumalea*			25	2	0	0
	Tipulidae	*Dicranota*	39	12	36	5	3	15
		Hexatoma	9	30				
		Hexatoma/Limnophila			25	0	0	0
		Limnophila			2	14	3	2
		Limonia			0	8	0	0
		Molophilus			0	10	0	0
		Ormosia/Erioptera	7	0				
		Tipulidae sp.	19	3	6	24	0	1

*these taxa were only found in one stream
**these taxa were only found in one stream-pair

Appendix III (Cont'd.)

Order	Family	Genus/taxa	forest type		season			
			YG	OG	sum	aut	win	spr
EPH	Baetidae	Baetidae sp.	50	33	19	16	29	18
		Baetis			22	0	27	25
		Diphetor			16	1	11	34
	Ephemerellidae	*Caudatella**			11	0	0	0
		Ephemerella/Serratella	17	0	30	0	0	0
		Ephemerellidae sp.			25	3	22	31
	Ephemeroptera sp.	Ephemeroptera sp.			2	26	6	3
	Heptageniidae	*Cinygma*			37	7	4	21
		Cinygmula			0	33	37	16
		Epeorus			5	14	33	25
		Heptageniidae sp.			12	26	15	19
		Ironodes			11	16	23	8
		*Rhithrogena***	16	4				
	Leptophlebiidae	*Paraleptophlebia*	45	53				
HAR	Harpacticoida sp.	Harpacticoida sp.	52	36	28	25	13	23
HEM	Gerridae	*Gerris***			8	0	0	0
HYD	Hydracarina sp.	Hydracarina sp.			28	25	19	27
NEM	Nematoda sp.	Nematoda sp.	51	30	18	32	15	16
ODO	Gomphidae	*Octogomphus***			8	0	0	0
OLI	Oligochaeta sp.	Oligochaeta sp.	53	45	25	28	24	22
PLE	Capniidae	Capniidae sp.			0	73	0	0
	Chloroperlidae	*Alloperla/Bisancora*			7	2	4	55
		Kathroperla			18	4	8	9
		Sweltsa			21	22	33	5
	Leuctridae	Leuctridae sp.			0	17	9	27
	Leuctridae/Capniidae	Leuctridae/Capniidae sp.			61	1	0	1
PLE	Leuctridae	*Paraleuctra*			0	4	26	5
	Nemouridae	*Malenka*	31	14	15	0	12	34
		Nemouridae sp.			32	28	7	21
		Ostrocerca			0	0	0	28
		Soyedina	26	9	18	20	2	1
		Visoka	7	33				
		Zapada			42	14	6	6
		Zapada/Malenka			0	0	24	25
	Peltoperlidae	Peltoperlidae sp.			0	18	29	38
		Soliperla	23	6	3	22	1	8
		Yoraperla			35	12	10	15
	Perlidae	*Calineuria*	13	36				
		Perlidae sp.	5	17	39	1	0	3
	Perlodidae	Perlodidae sp.	21	1				
	Plecoptera sp.	Plecoptera sp.	47	34	35	27	7	18
	Pteronarcyidae	*Pteronarcella**	7	0				
PRO	Pleuroceridae	Hydrobiidae sp.			15	29	23	17
		*Juga***	3	19				

*these taxa were only found in one stream
**these taxa were only found in one stream-pair

Appendix III (Cont'd.)

| Order | Family | Genus/taxa | forest type | | season | | | |
			YG	OG	sum	aut	win	spr
TRI	Glossosomatidae	*Anagapetus*			0	29	13	0
		Glossosomatidae sp.			11	6	0	0
	Goeridae	*Goeracea*	7	1	1	0	0	9
	Hydropsychidae	Hydropsychidae sp.			15	1	0	0
	Lepidostomatidae	*Lepidostoma*	13	45	25	10	10	11
	Limnephilidae	*Philocasca*	7	0				
	Philopotamidae	*Dolophilodes*			7	8	1	14
		Philopotamidae pupae			14	0	0	0
		Philopotamidae sp.	31	16				
	Rhyacophilidae	*Rhyacophila*			15	30	24	18
		Rhyacophila pupae	7	0	8	0	0	1
	Trichoptera sp.	Trichoptera sp.			7	43	5	1
	Uenoidae	*Neophylax*			20	0	10	17
		*Neothremma**	8	0				
		Uenoidae sp.			0	7	25	18

*these taxa were only found in one stream
**these taxa were only found in one stream-pair

Appendix IV Indicator Species Analyses values for emergent taxa demonstrating differences ($p \leq 0.05$) between forest types, or among seasons. Indicator values (% of perfect indication) were derived by combining values of relative abundance and relative frequency (Dufrene and Legendre 1997). Significance of group membership was determined through 1000 Monte Carlo simulations. DIP = Diptera, EPH = Ephemeroptera, HEM = Hemiptera, PLE = Plecoptera, TRI = Trichoptera. YG = young growth, OG = old growth. Values are listed only for significant differences between forest types, seasons, or both. These 52 taxa represent 54.7% of the total number of taxa evaluated with Indicator Species Analysis.

| Order | Family | Genus/taxa | forest type | | season | | | |
			YG	OG	sum	aut	win	spr
DIP	Ceratopogonidae	Ceratopogonidae sp.			48	0	0	3
	Chironomidae	Chironomidae sp.	49	39	29	23	11	23
	Chironomidae/ Ceratopogonidae	Chironomidae/ Ceratopogonidae sp.			30	25	2	13
	Culicidae	*Culex*			10	0	0	0
	Dixidae	*Dixella*			19	1	0	0
	Dolichopodidae	Dolichopodidae sp.			8	0	0	0
	Empididae	*Chelifera*			10	0	0	0
		Neoplasta			6	0	0	0
		Oreogeton*	7	0	13	0	0	0
		Oreothalia			19	0	0	0
	Psychodidae	Psychodinae sp.			18	0	0	1
	Tipulidae	*Lipsothrix*			8	0	0	0
		Molophilus			11	0	0	0
		Pedicia			0	0	8	16
		Pilaria			6	0	0	0
		Tipulidae sp.			15	0	0	0
EPH	Ameletidae	*Ameletus*			14	0	0	2
	Baetidae	Baetidae sp.			2	1	0	9
		Baetis			9	0	0	6
	Ephemerellidae	*Drunella*			8	0	0	0
		Ephemerellidae sp.			13	0	0	0
	Ephemeroptera sp.	Ephemeroptera sp.			7	0	0	0
	Heptageniidae	*Cinygma*			42	1	0	0
		Epeorus			0	0	0	6
		Heptageniidae sp.			10	0	0	1
		Ironodes	13	2	1	0	0	31
	Leptophlebiidae	*Paraleptophlebia*			59	1	0	2
HEM	Gerridae	*Aquarius*			0	0	11	13
PLE	Capniidae	*Paracapnia*			0	0	24	4
	Chloroperlidae	*Alloperla/Bisancora*			47	0	0	2
		Sweltsa			6	0	0	2
	Leuctridae	*Despaxia*			0	33	4	1
		Moselia			16	0	0	34
		Paraleuctra			3	0	21	4
	Nemouridae	*Malenka*			38	2	0	1
		Ostrocerca			5	0	0	10
		Soyedina			6	0	0	26
		Visoka**			0	0	0	6
		Zapada			4	0	6	16
	Peltoperlidae	*Soliperla***			6	0	0	0
		Yoraperla			32	0	0	1

*these taxa were only found in one stream
**these taxa were only found in one stream-pair

Appendix IV (Cont'd)

| Order | Family | Genus/taxa | forest type | | season | | | |
			YG	OG	sum	aut	win	spr
PLE	Perlidae	*Calineuria*			8	0	0	0
	Perlodidae	*Calliperla*			6	0	0	0
TRI	Brachycentridae	*Micrasema*			9	0	0	0
	Glossosomatidae	*Anagapetus*	0	6	5	0	0	3
	Goeridae	*Goeracea**			0	0	0	6
	Lepidostomatidae	*Lepidostoma*			19	0	0	0
	Philopotamidae	*Dolophilodes*			46	0	0	6
		Wormaldia	4	22	6	3	2	15
	Polycentropodidae	*Polycentropus**	6	0	10	0	0	0
	Rhyacophilidae	*Rhyacophila*	15	3	24	0	0	6
	Uenoidae	*Neophylax*			0	22	0	0

*these taxa were only found in one stream

**these taxa were only found in one stream-pair

Appendix V Mean top three most abundant emergent taxa during each collection period. Values are proportions of total emergence (No. individuals m^{-2} day^{-1}) during each period. Chiron./Cerato sp. = Chironomidae/Ceratoponidae sp.

date	WS-1		WS-2		N.B.		Anderson		WS-7		WS-8	
6/30/2003	Chironomidae sp.	36.5	Chironomidae sp.	53.0	Chironomidae sp.	46.9	Chironomidae sp.	38.6	Ceratopogonidae sp.	18.7	Chironomidae sp.	36.7
	Paraleptophlebia	33.1	Chiron./Cerato. sp.	15.4	Ceratopogonidae sp.	7.6	Chiron./Cerato. sp.	14.3	Chiron./Cerato. sp.	15.9	*Alloperla/Bisancora*	12.3
	Dolophilodes	5.7	*Dolophilodes*	6.7	*Dolophilodes*	7.1	*Alloperla/Bisancora*	9.5	Chironomidae sp.	12.3	Ceratopogonidae sp.	10.6
7/16/2003	Chironomidae sp.	23.8	Chiron./Cerato. sp.	55.0	Chiron./Cerato. sp.	34.5	Chiron./Cerato. sp.	28.9	Chironomidae sp.	35.2	Chironomidae sp.	34.9
	Dolophilodes	21.9	Chironomidae sp.	21.7	Chironomidae sp.	26.4	Chironomidae sp.	25.3	Chiron./Cerato. sp.	11.7	Chiron./Cerato. sp.	21.1
	Chiron./Cerato. sp.	12.4	*Paraleptophlebia*	8.3	*Paraleptophlebia*	7.2	*Paraleptophlebia*	24.1	Ceratopogonidae sp.	6.3	*Paraleptophlebia*	11.3
7/30/2003	*Malenka*	21.9	Chiron./Cerato. sp.	39.2	Chiron./Cerato. sp.	36.1	Chironomidae sp.	45.4	Chironomidae sp.	29.0	Chironomidae sp.	25.6
	Ceratopogonidae sp.	18.1	Chironomidae sp.	32.3	Chironomidae sp.	26.1	Chiron./Cerato. sp.	22.7	*Malenka*	24.4	*Malenka*	22.7
	Dolophilodes	15.2	*Malenka*	13.1	*Dolophilodes*	10.0	*Dolophilodes*	6.4	Ceratopogonidae sp.	15.3	Chiron./Cerato. sp.	13.2
8/13/2003	*Paraleptophlebia*	25.9	Chironomidae sp.	41.0	Chironomidae sp.	29.0	*Dolophilodes*	24.6	*Malenka*	33.9	*Dolophilodes*	37.0
	Malenka	18.5	Chiron./Cerato. sp.	34.6	Chiron./Cerato. sp.	16.1	Chironomidae sp.	16.4	Chironomidae sp.	16.9	Chironomidae sp.	19.0
	Ceratopogonidae sp.	11.1	*Malenka*	5.1	*Rhyacophila*	9.7	Chiron./Cerato. sp.	14.8	*Dolophilodes*	15.3	Chiron./Cerato. sp.	17.0
8/28/2003	Chironomidae sp.	28.9	Chiron./Cerato. sp.	34.4	Chironomidae sp.	47.1	Chiron./Cerato. sp.	27.5	Chironomidae sp.	35.1	Chironomidae sp.	44.7
	Malenka	26.3	Chironomidae sp.	34.4	*Rhyacophila*	8.8	Chironomidae sp.	23.5	*Malenka*	10.4	Chiron./Cerato. sp.	13.8
	Psychodinae sp.	13.2	*Dolophilodes*	4.3	*Philocasca*	8.8	*Paraleptophlebia*	9.8	*Wormaldia*	7.8	*Malenka*	12.8
10/2/2003	*Despaxia augusta*	70.3	Chiron./Cerato. sp.	36.4	*Despaxia augusta*	39.5	*Despaxia augusta*	39.1	*Despaxia augusta*	31.4	*Despaxia augusta*	68.7
	Chironomidae sp.	10.8	Chironomidae sp.	23.5	Chironomidae sp.	21.1	Chiron./Cerato. sp.	32.6	Chironomidae sp.	25.5	Chironomidae sp.	15.0
	Chiron./Cerato. sp.	5.4	*Despaxia augusta*	23.5	Chiron./Cerato. sp.	18.4	*Neophylax*	8.0	*Paraleptophlebia*	9.8	Chiron./Cerato. sp.	10.0
11/14/2003	Chiron./Cerato. sp.	40.5	Chironomidae sp.	39.3	Chironomidae sp.	69.6	Chironomidae sp.	40.0	Chironomidae sp.	52.2	Chironomidae sp.	45.5
	Chironomidae sp.	35.1	Chiron./Cerato. sp.	35.7	Chiron./Cerato. sp.	17.4	Chiron./Cerato. sp.	30.0	*Clinocera*	21.7	Chiron./Cerato. sp.	27.3
	Clinocera	18.9	*Clinocera*	10.7	*Clinocera*	8.7	*Wormaldia*	20.0	Chiron./Cerato. sp.	13.0	Hexatomini sp.	9.1

Appendix V (Cont'd.)

date	WS-1		WS-2		N.B.		Anderson		WS-7		WS-8	
12/30/2003	Chiron./Cerato. sp.	100.0	-		Heterlimnius	33.3	Aquarius	50.0	Paracapnia disala	100.0	Despaxia augusta	100.0
					Zapada	33.3	Paracapnia disala	50.0				
					Paracapnia disala	33.3						
3/13/2004	Chironomidae sp.	43.1	Aquarius	42.3	Chironomidae sp.	68.1	Chironomidae sp.	34.2	Wormaldia	30.4	Paracapnia disala	36.0
	Chiron./Cerato. sp.	17.2	Pedicia	30.8	Zapada	19.1	Paraleuctra	20.8	Chironomidae sp.	21.7	Chironomidae sp.	20.0
	Pedicia	12.1	Paraleuctra	15.4	Clinocera	4.3	Aquarius	8.1	Zapada	17.4	Despaxia augusta	12.0
							Wormaldia	8.1				
							Zapada	8.1				
4/11/2004	Chironomidae sp.	30.6	Aquarius	28.0	Chironomidae sp.	30.9	Chiron./Cerato. sp.	37.8	Chironomidae sp.	26.8	Moselia	41.2
	Ironodes	19.4	Pedicia	22.0	Pedicia	21.0	Chironomidae sp.	24.3	Zapada	19.6	Chironomidae sp.	29.4
	Chiron./Cerato. sp.	16.1	Chironomidae sp.	14.0	Moselia	16.0	Pedicia	23.0	Paracapnia disala	12.5	Soyedina	7.8
5/9/2004	Chironomidae sp.	47.5	Chironomidae sp.	26.9	Chironomidae sp.	58.1	Chironomidae sp.	68.7	Soyedina	21.7	Chironomidae sp.	57.7
	Alloperla/Bisancora	10.6	Aquarius	11.5	Ironodes	10.8	Prosimulium	6.1	Chironomidae sp.	21.7	Despaxia augusta	9.9
	Ironodes	8.6	Anagapetus	9.6	Moselia	5.4	Ceratopogonidae sp.	5.3	Moselia	13.0	Zapada	7.0
	Chiron./Cerato. sp.	8.6	Chiron./Cerato. sp.	9.6								
			Ironodes	9.6								
5/31/2004	Alloperla/Bisancora	35.1	Chironomidae sp.	33.2	Chironomidae sp.	29.7	Chironomidae sp.	47.2	Alloperla/Bisancora	27.5	Chironomidae sp.	44.7
	Chironomidae sp.	30.2	Alloperla/Bisancora	22.5	Chiron./Cerato. sp.	12.8	Chiron./Cerato. sp.	27.9	Chironomidae sp.	15.7	Chiron./Cerato. sp.	40.4
	Chiron./Cerato. sp.	7.9	Chiron./Cerato. sp.	16.0	Yoraperla	9.5	Alloperla/Bisancora	7.0	Soyedina	13.7	Wormaldia	6.4
6/30/2004	Paraleptophlebia	35.4	Chiron./Cerato. sp.	28.2	Chironomidae sp.	30.5	Chironomidae sp.	36.0	Chironomidae sp.	23.1	Chironomidae sp.	39.5
	Chiron./Cerato. sp.	33.3	Alloperla/Bisancora	25.8	Alloperla/Bisancora	17.2	Chiron./Cerato. sp.	29.7	Paraleptophlebia	14.1	Paraleptophlebia	17.1
	Chironomidae sp.	9.5	Malenka	8.9	Malenka	14.6	Malenka	9.2	Ceratopogonidae sp.	12.8	Chiron./Cerato. sp.	14.5

Note: Complete benthic and emergent macroinvertebrate data can be reviewed and downloaded at the following URL:

www.fsl.orst.edu/lter