The Influence of Forest Management on Stream Communities in the Upper Peninsula of Michigan

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ABSTRACT

We examined the relationships among selection logging and headwater stream macroinvertebrate communities, stream habitat and benthic organic matter dynamics in the Otter River watershed, an Upper Midwest watershed of Lake Superior. We sampled macroinvertebrates and benthic organic matter (BOM), before and after fall leaf-off and surveyed physical habitat conditions at nine study streams. We found a positive relationship between the number of years post logging in forest stands adjacent to study sites and Plecopteran biomass and density. Years post adjacent logging was positively related to study site canopy cover, substrate size and fall benthic organic matter standing stock. In contrast to local study site scale observations, we detected no generalized relationships between the history of logging at the catchment scale and study site physical, or BOM variables or macroinvertebrate community structure. BOM standing stocks correlated positively with upstream and study site canopy cover, suggesting that local and upstream canopy may be a strong determinant of organic matter dynamics at the local scale. BOM standing stock maxima in the fall was positively related to the density and biomass of Plecopteran shredders and shredder density in the summer, suggesting that organic matter availability may be constraining the summer shredder community. Food limitation and habitat alterations (e.g., smaller substrate size) across our sites may have influenced the composition of shredder communities to favor the large Dipteran shredder, Tipula sp. over Plecopteran shredders. In many cases, the biomass and density of macroinvertebrate functional groups were correlated with study site catchment area, which may indicate that communities are strongly linked with upstream processes across our sites. Our results suggest that selection logging in the Otter River Watershed may influence quantitative aspects of riparian stream communities and ecosystem processes at the reach scale. The extent of alteration to riparian aquatic ecosystems by selection logging in this northern hardwood ecosystem is uncertain.

INTRODUCTION

Forested headwater streams are connected physically and biologically to surrounding watersheds by the transport of water, organic matter, nutrients and sediments (Hynes1975). The upland and riparian forests within these watersheds play a vital role in the mediation of water quality, stream physical conditions (Naiman et al. 1993, Allan and Johnson 1997, Naiman and Decamps 1997), and habitat for coldwater fishes and invertebrates (Murphy et al. 1986). Logging and road building within headwater catchments can create a range of disturbances potentially influencing patterns in the structure of stream biological communities and the functioning of key ecosystem processes (Borman and Likens 1977, Huryn 2000). Conditions across the watershed (Richards and Minshall, 1992, Townsend et al. 1997, Harding et al. 1998), upstream bioprocessing and geomorphology (Vannote et al. 1980), local in-stream, physical habitat and organic matter dynamics (Statzner and Higler 1986, Smock et al. 1989, Wallace et al 1993, Hall et al 2001), effectively act as filters, determining local biological community composition from regional species pools (Sensu: Tonn 1990, Poff 1997). Aquatic macroinvertebrates (primarily insects) provide important ecosystem functions in headwater streams including processing organic matter and providing food for fishes and riparian birds.
Thus, knowledge of macroinvertebrate ecology and status has been suggested to be critical for effective long-term management of streams (McCafferty 1983). The nature of these biotic-abiotic interrelationships and the key role of macroinvertebrates in headwater streams have prompted the use of macroinvertebrates as effective biological indicators of the general health of the stream ecosystems (Karr 1999). Many macroinvertebrate metrics have been found to be sensitive to the range of disturbances in streams draining logged watersheds (Fortino et al 2004). Stream macroinvertebrate communities encompass a diverse range of trophic requirements (Cummins and Klug 1979) and levels of tolerance to anthropogenic disturbance (Hilsenhoff 1977). The distribution of these requirements within communities can be used as an indirect measure of overall stream condition over time and have been used in combination as measures of overall stream health (Karr 1999). There is a concern however, that effective assessment of stream condition must also include direct measures of stream ecosystem processes (Gessner and Chauvet 2002). The selection of practical and effective measures of stream ecosystem processes is a major challenge; however recent research has allowed us to understand much more clearly how stream processes in forested watersheds interact naturally and with anthropogenic influences across a range of spatial and temporal scales (Wallace et al 1997, Webster et al 1999).

Recent research from large-scale and generally less-mechanistically based approaches (e.g., geographical information system based) and local-scale studies have documented compelling relationships between stream communities and the history of land use within watersheds (e.g., Richards et al. 1996, Allan and Johnson 1997, Wang et al. 1997). A rich literature on research conducted largely in forests under even-aged management (e.g., clear cutting) of the Pacific northwest region of the United States and Canada suggests that logging and associated road building activities in riparian zones can alter the landscape in ways that adversely affect aquatic habitat (Murphy et al. 1986, Chamberlin et al. 1991, Swanson and Franklin 1992) and alter ecosystem processes (Brosofske et al. 1997, Naiman et al. 2000). Movement of machinery and the building of roads to facilitate logging can greatly increase sediment input to streams (Gucinski et al 2000), which can embed streamed substrate and degrade habitat for many coldwater species (Stednick and Kern 1994, Waters 1995). Logging can lead to decreased canopy cover and increased stream temperatures (Brown and Krygier 1970, Barton et al. 1985, Hornbeck and Kochenderfer 2000) and it may alter organic and inorganic runoff into streams and stream flow rate (Patric 1978, Hornbeck et al. 1993). Logging can also result in reduced abundances of large instream woody debris (LWD), which may alter habitat complexity (Bilby 1981, Bilby and Ward 1991; Quinn and Peterson 1996).

This potential influence of logging on stream and riparian biota has been extensively documented for western forests (e.g., Merten and Newman 2000); however, little information addressing the potential influence of logging in the Great Lakes Region is available. Headwater streams may represent approximately 95% of the total channel length in a typical watershed (Sweeny 1993) and although the importance of these tributary streams to the long-term maintenance of the Great Lakes is often acknowledged (e.g., MDEQ 1998a), their role in management and research in the Great Lakes region has been under-emphasized (Hayes and Petrusso 1999). There is a strong need to understand the impacts of the prevailing forest management practices in the Upper Midwest on headwater stream habitat, organic matter dynamics and biological community composition.

The application of conclusions from western studies for prediction of the potential associations between land use and stream communities in the upper Great Lakes region may be
limited by differences in geological history, climate, topography, species composition and logging practices relative to those outside of this region. For example, in the Upper Midwest gradient is frequently lower and climatological conditions are temporally more even than those in many areas of the west. In addition, many past studies have focused on the effect of clear cutting on stream biota and habitat (e.g. Golladay et al. 1989), whereas much of the forest management in the Upper Midwest consists of selection logging of discrete stands of northern hardwoods. Approximately 88% of the western Upper Peninsula of Michigan is forested and northern and mixed-hardwood forests account for 54% of total forest cover (Leatherberry and Spencer 1996). Since the mid-twentieth century, selection logging (single-tree or group-tree selection or uneven-age management; Society of American Foresters 1981) has replaced clear-cut logging as the major forest management technique in many northern hardwood forests (Smith 1962; Seymour 1995).

Little is known about the potential effects of less intensive and presumably more benign forms of timber harvest such as selection logging on aquatic communities. Taft (1992) suggested that erosion and sedimentation related to historical and ongoing selection logging has adversely impacted the biological integrity and physical habitat conditions of Otter River tributaries in the Upper Peninsula of Michigan. In this same system, the history of selection logging quantified as the years since adjacent forest stands had been selection logged, appeared to be related to stream community and riparian bird community composition (Flaspohler et al. 2002) and was positively related to the abundance of brook trout (*Salvelinus fontinalis*) in these streams (VanDusen et al. in press).

If, for example, selection logging is associated with increased erosion and sedimentation in streams, the energetic and organic base of the aquatic food web could also be altered. By filling interstices between inorganic substrate, sediment effectively smoothes the streambed and greatly reduces the efficiency of streams to retain organic matter (Webster 1994, Lamberti and Berg 1995). Macroinvertebrate communities in forested headwater streams are highly dependent on allochthonous organic matter, mainly in the form of seasonal leaf litter inputs from riparian vegetation (Vannote et al. 1980; see review in Dobson 1992). A critical aspect of instream organic matter availability is its retention in localized areas so that it can be consumed or processed by resident organisms (Brookshire and Dwire 2003). Past studies have shown that retention of organic matter, in addition to leaf litter inputs, plays a significant role in structuring stream macroinvertebrate communities (Prochazka et al. 1991). Many of the stream properties conducive to retention are complex and synergistic. Disturbances to streams can alter these relationships and reduce the critical ability of streams to retain and process allochthonous inputs, and the effects of these alterations may persist for centuries (Webster 1994). Streams in undisturbed, forested watersheds typically have dense canopy cover, low primary production and a benthic community dominated by detritivores, of which leaf shredding invertebrates are a major component (Vannote et al. 1980). As a result, the base of ecosystem structure and energy flow in these streams can be formed by inputs of organic matter from riparian forests (Vannote et al 1980). The dynamics of organic matter input, retention and bioprocessing can thus be seen as a logical focus for metrics of stream ecosystem process (Gessner and Chauvet 2002) and they were a major component of this study.

In this study we examined the interrelationships between watershed and land use characteristics (e.g., selection or partial logging) in northern, mixed-hardwood forests and patterns of benthic habitat and macroinvertebrate community structure and ecosystem processes in adjacent headwater streams. We examined the broad and general hypothesis that watershed
conditions and the history of land use in the form of logging in forest stands adjacent to headwater streams was related to stream habitat conditions and aquatic macroinvertebrate communities (Fig. 1). Specifically we examined the hypotheses that:

- study sites in catchments and/or adjacent to forest stands that were most recently logged would have reduced habitat quality, including substrates with more fine sediment, than those with a greater number of years post logging (Figs 1 and 2),
- study sites with reduced habitat quality such as increased sediment would contain reduced benthic organic matter standing stocks (Fig. 2),
- lower levels of benthic organic matter standing stocks would be associated with reduced overall invertebrate abundance and biomass (Fig. 2),
- levels of benthic organic matter standing stocks and physical habitat quality would be associated with the invertebrate community structure including functional and taxonomic composition. For example, abundances of leaf shredding functional group would be greater in streams with more course benthic organic matter (Fig. 2).
- catchment and/or adjacent logging history (e.g., years since logging had occurred along a comparative chronoseqence of study sites) would be associated with increased relative abundance of disturbance tolerant taxa (Fig. 3)

Research to examine these predictions was conducted at the spatial scales of the stream reach, upstream section and catchments of headwater streams in the Otter River watershed, located in Michigan’s Upper Peninsula.
METHODS

Study site selection

This study was conducted in the Otter River watershed, located in Michigan’s Upper Peninsula in Houghton, Baraga and Ontonagon Counties (Fig. 4). Land cover in the watershed is 89.1% forested, 5.4% agricultural, 3.5% roads, 2.0% wetlands (Lutz 1993). There is a mixture of land ownership within the watershed of State forest land, commercial logging, and small private holdings. Selection logging is the dominant land use throughout the watershed. All study sites were located either on state forest land or private land administered under the Michigan Certified Forestry Act (CFA), which requires best management practices (BMP’s) in exchange for tax incentives. Prior to the 2001 field season, we identified nine accessible second-order streams with riparian forests managed under CFA within the watershed. Study sites were positioned on each of these streams and consisted of a 100m reach located at least 100m upstream from road crossings and selected to include a variety of channel units (riffles runs and pools). Study sites encompassed a range of 2-11 years since last being selection logged (Table 1). As a result of beaver activity during the first year, one site was lost from our study; site was replaced with Small Bear Creek, which had more difficult access than the other streams.

Hierarchical survey

In 2001 and 2002 a multi-scale survey of physical and biological variables was conducted at each study stream (Table 2). Reach-scale surveys of macroinvertebrates and physical variables were conducted within 100m study sites in 2001 and 2002. In 2001, meso-scale physical variables were estimated within the 1km upstream section above each study site. At the largest scale, variables were estimated as area weighted means across the catchment of each study site using GIS.

Study site surveys

Macroinvertebrate assemblage

The macroinvertebrate assemblage at each study site was surveyed seasonally (early summer, late summer and fall) in 2001 and 2002. The early summer samples were collected June 12-19, which was the earliest that roads were passable providing access to study sites. Because of the replacement of study sites that occurred during the 2001 sampling period, these initial macroinvertebrate data are not available for one study site (Small Bear Creek). Late summer sampling took place in August 13-26 (before leaf-off in the surrounding forests) and fall sampling occurred October 22 – November 18 (after leaf-off). Early and late summer samples were collected during low stream flow conditions. More frequent precipitation events resulted in fall hydrological conditions being more variable. During each survey, three haphazardly located Hess samples were collected in riffle areas within each study site. Samples were preserved in 10% formalin in the field and returned to the lab for processing. All individuals were picked from 90% of samples (n=148), the remainder of samples (n=17) were split to 0.25 or 0.5 using a Folsom plankton splitter. All of the samples processed by technicians were checked by senior personnel for quality assurance. Macroinvertebrates from all samples were identified (mainly to genus level) and assigned to functional and trophic groups according to Hillsenhoff (1995) and Merritt and Cummins (1996). Within each sample, the total body lengths of thirty individuals from each taxonomic group were measured using a dissecting microscope with a drawing tube and digitizing board. Biomass of each individual was estimated using published length-mass regressions (Benke et al 1999) when available (n = 117). When appropriate, published
regressions for taxonomically related taxa or life stages were substituted for regressions not in the literature. All published length-mass regressions measured as dry mass were converted to AFDM using percent ash estimations of closely related taxonomic or functional feeding groups from Benke et al (1999). For each of the remaining taxa for which length-mass regressions were not available (n = 22) we measured the total lengths of 30 individuals from a range of body sizes, oven dried them (48 hours at 50°C), ashed them in a muffle furnace (4 hours at 550°C), re-wetted with distilled water, oven dried them for 24 hrs, desiccated for 24 hrs, and individually weighed them on a Kahn micro balance to determine ash free dry mass (AFDM). Length-mass regressions (Appendix A) were then developed using Proc Regression (Statistical Analysis System 8). A table of length-mass regressions, dry mass to ashfree dry mass conversions and substitutions for sampled taxa is available upon request. Mean biomass and density of macroinvertebrates within taxonomic and functional feeding groups were then estimated for each study site.

Benthic organic matter standing stocks

Benthic Organic Matter (BOM) samples were collected within each study site in the late summer and fall to coincide with periods of predicted yearly minimum and maximum BOM. We used a 25cm diameter hydraulic benthos sampler (Brown et al. 1987) with a 350µm mesh filter to sample BOM throughout each study site. During the operation of this sampler, an electric pump moved water and debris collected from within the sample cylinder through a filter and the discharge water was used to stir the sediments on the stream bottom within the cylinder. Three samples were collected from two channel units of each type (riffles, runs, pools) for a total of eighteen samples per study site per sampling period. Three samples were collected along a transect across the middle of the channel unit, one in the thalweg and the other two samples midway between the thalweg and each stream bank. Sampling was standardized by first pushing the cylindrical base of the pump apparatus into the sediment, reaching in and collecting any large leaves or sticks on the substrate surface. After this initial collection of debris, the pump was operated for two minutes and then the sediment on the bottom was stirred by hand to a depth of approximately 10cm and the pump/filter was operated for an additional two minutes. Samples were preserved in 10% formalin and returned to the lab for processing. BOM size fractions were sieved into fractions of 500-1000µm (fine benthic organic matter; FBOM) and greater than 1000µm (course benthic organic matter; CBOM). Prior to further processing, wood and large invertebrates were removed from the CBOM fraction. The smallest size fraction (350-500µm) was not processed. Samples were dried in a drying oven (48 hr at 50°C), ashed (4hr at 550°C), re-wetted with distilled water, oven dried for 24 hrs, desiccated for 24 hrs, and weighed to determine the ash free dry mass (AFDM) of each size fraction. BOM standing stock values were characterized in a number of ways. Densities of each size fraction (CBOM and FBOM) as well as total benthic organic matter (TBOM) were determined within riffle, runs, and pools and across the study site by taking the mean of sample density values by year as well as season. Seasonal values were determined by calculating the mean of seasonal sampling periods (late summer or fall) for size fractions and channel units across the two years of the study. Yearly BOM values were determined by calculating the mean of seasonal sample values within years and then determining the mean of values from the two years.
Habitat survey

We conducted extensive surveys of the physical habitat of each study stream during low-flow conditions in 2001 (table 2). We measured the number and area of channel geomorphic units (CGU: riffles, runs and pools) based on Hawkins et al. (1993). In riffle areas, we determined the percent of substrate within the streambed composed of fine particles (< 2 mm) using the “shovel method” (Hames et al. 1996). We quantified surface substrate size characteristics within each channel unit using the “pebble count” method (Potyondy and Hardy 1994). Within each CGU type we selected and measured at least sixty rocks randomly selected if they contacted a specific point on one boot as we walked along a zigzag transect diagonal to the stream bank. We calculated the median substrate size for each CGU type and then area-weighted these values by the total area of each CGU type to determine the mean substrate size for the entire study site.

Discharge was estimated using a Marsh McBirney digital water velocity meter across a transect chosen based on the appearance of laminar flow. Water surface slope was measured along the 100-m study site using an Abney level following the protocol of Issak et al. (1998). Water temperature was continuously monitored by submerged temperature data loggers deployed at each study site as soon as roads were passable. Temperature data used in our analysis represents a period of uniform coverage across study sites and years from June 18 to October 21, 2001. Canopy cover was measured using a sighting tube at one meter intervals along three transects across the stream’s wetted width located at 25, 50 and 75% of study site length. The area of canopy cover for each study site was quantified by multiplying the mean percent of canopy across transects by the total stream surface area to derive the total site area in canopy cover. At each of these three transects we also measured bank-full height, bank-full and wetted width. We measured woody debris aggregate length and width and calculated individual aggregate area and total area of woody debris within study site.

In addition to the previously described quantitative assessments, we also conducted an integrative habitat assessment using the habitat assessment portion of the Great Lakes and Environmental Assessment Section (GLEAS) procedure 51 (MDEQ 1998b). For standardization of our GLEAS habitat assessment, we worked with William Taft and Neil Godby (MDEQ) for one day as they assessed two stream systems in the Upper Peninsula. Values used in this analysis were the total of habitat assessment scores for each study site. We estimated the number of years since adjacent forest stands were last logged (adjacent logging) using 1:24,000 digital State and commercial forest management maps (Michigan Department of Natural Resources and Heartwood Forestland Group) in a geographic information system (GIS; ArcView and Arc Info). When study sites had adjacent forest stands of differing logging history on each bank, the years since most recent logging used in our analysis was calculated as the mean of the two values.

Upstream survey

A survey of physical variables across the 1km upstream section above each study site was carried out during low-flow conditions, July 9 to August 22, 2001. Physical variables assessed included a subset of variables measured within the 100m study site (Table 2). Conditions across the upstream section were estimated by surveying variables within five consecutive 200m upstream compartments. Each upstream compartment was sub-sampled by measuring physical variables within the 200m compartment means of these upstream compartments were calculated.
**Catchment scale survey**

Watershed slope and boundaries of study site catchments were determined using 1:24,000 scale USGS Digital Elevation Model (DEM) maps. We estimated the number of years post logging across study site catchments (catchment logging) by first determining the values for individual stands using 1:24,000 digital forest management stand maps (described earlier) and then weighted these values by their proportional stand area and summed these weighted stand values. We constructed a map of ground water influence using Darcy’s law to predict groundwater velocity for each study site catchment. This map was constructed using GIS to overlay layers of slope (1:25,000 digital elevation model; DEM) and quaternary geology (1:250,000; USGS). Values for slope were then multiplied by the hydrologic conductivity values associated with each quaternary material. Catchment ground water velocity values were determined by area-weighting and summing distributed values.

**Analysis**

Data base management and statistical analysis was performed using Statistical Analysis System (SAS) software. Analysis included the use of the Proc Summary, Proc Means and Proc Regression commands. Relationships between variables were estimated by regression analysis, carried out using Sigma Plot software. A type one error ($\alpha$) of 0.05 was used to reject null hypothesis.
RESULTS

Macroinvertebrate composition

During this study, we detected 111 genera of macroinvertebrates in 56 families in study site riffle zones of the nine headwater streams (see Appendix A for a complete taxa list). These invertebrates were primarily members of six orders that are known to be common in headwater streams (Merritt and Cummins 1996; Fig. 5). Within this taxonomic assemblage, 51-67% of total seasonal biomass and 32-58% of total seasonal abundance were members of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT). Across the study sites, EPT mean values ranged 25-88% of total biomass and 48-79% of total density. Net spinning caddisflies (e.g., Hydropsychidae) formed the majority of EPT taxa biomass during all three sampling periods. While these caddisflies were major contributors to the total EPT biomass, they were a minor component of EPT density due to their generally large individual size. Late summer EPT densities were elevated relative to other times of year by abundant small mayflies (e.g., *Baetis* sp. and *Paraleptophlebia* sp.), which were detected in larger numbers in samples from late summer relative to their abundance during the other sampling periods.

In addition to taxonomic identification, we categorized macroinvertebrates into functional feeding groups (i.e. predators, collector-gatherers, collector-filterers, shredders and grazers). Collectors (filterers and gatherers) were in general the biomass and numerical dominants in early- and late summer and fall surveys (Fig. 6). Predators were the second most abundant functional group of invertebrates, which accounted for 21-29% of the total biomass seasonally (Fig. 6a). Seasonal and yearly patterns of relative composition within functional groups varied in some instances depending on whether enumeration was based on density or biomass. For example, approximately 24-36% of total predator biomass was large-bodied Odonates (primarily *Cordelegaseter* sp. and *Boyeria* sp.); however, Odonates were less than 2% of the total number of predators we collected. Taxa within the shredder functional group displayed the largest disparity between their relative contributions to total biomass and total density. Seasonally, the large-bodied burrowing Diptera *Tipula* sp. constituted 4-10% of the overall total invertebrate biomass and 72-79% of the shredder functional group biomass, but less than 1% of the total overall invertebrate density and 0.7-3% of the shredder density. On a seasonal basis, Plecopteran shredders were less than 1% of mean overall total invertebrate biomass and 8-25% of the mean shredder biomass yet they were 3-10% of mean overall total invertebrate density and 60-85% of mean shredder density. The large body size and low relative sample densities of *Tipula* sp. made their relative impact on biomass much greater than their relative contribution to shredder functional group density. In addition to these differences in enumeration, physiological, behavioral and life history traits (described below) may interact with selective stream conditions favoring *Tipula* sp. or Plecopteran shredders at some study sites. Contrasts between these members of the shredder functional group may be seen in the correlation between several study site and catchment physical variables and the ratio of *Tipula* sp. to Plecopteran spp. biomass (shown below). For these reasons, we analyzed abundances of “Plecopteran shredders”, in addition to the complete shredder functional group throughout our analysis to more thoroughly describe biological and physical relationships across study sites. The third most dominant shredder taxa, in terms of biomass, were Trichoptera in the genus *Lepidostoma* sp., which made up 0.4-2.9% of shredder biomass seasonally.
Benthic organic matter

As would be expected there was strong seasonal variation in the standing ash free dry mass of each BOM size fraction with greater standing biomass in the fall after leaf off, most of which was >2mm CBOM (Fig. 7a). Mean densities of CBOM were 82.5% higher in the fall than the summer, while FBOM was 63.3% higher in the fall. Overall there was a 79.3% increase in TBOM standing stocks in the fall. Comparisons across study sites and channel units showed pools contained the highest mean density of BOM during both sampling periods, while riffles were intermediate between pools and runs in terms of CBOM and TBOM standing stock across seasons (Fig. 7b). TBOM density ranged 30.4 – 108.4 g*m\(^{-2}\) across sites in the fall and 7.8 – 49.4 g*m\(^{-2}\) in the summer. Fall FBOM was correlated to mean summer TBOM, FBOM and CBOM; however there were no relationships between fall CBOM and any BOM standing stock variables in the summer (P> 0.45).

Relationships between logging and invertebrates, stream habitat, and organic matter

The gradient in years post logging of adjacent forest stands (adjacent logging) was not correlated with any yearly mean values of invertebrate biomass or density either by taxonomic or by functional groupings. However, there were a number of relationships between adjacent logging and macroinvertebrate community structure seasonally. For example, the number of years post logging was positively related to both mean late summer shredder density (Fig. 8a, P=0.044) and the biomass of late summer Plecopteran shredders (Fig. 8b, P=0.0015). The overall shredder biomass did not appear to be related to adjacent logging history seasonally (P > 0.45) or yearly (P > 0.17).

Adjacent logging was related to average median substrate size in study sites such that streams flowing through more recently logged forests generally had smaller diameter substrate material (Fig. 9a, P=0.055). However, one stream (Lake Fifteen Creek) had the smallest median substrate size of the study sites yet its adjacent forest had not been logged for nine years. This is a relatively low gradient stream (Table 1) and thus likely to have greater retention of fine substrate and sediments. The total area of vegetation canopy overlying the wetted stream channels of more recently logged sites was also less abundant (Fig. 9b, P=0.025). In addition to relationships with canopy cover and stream substrate, aspects of benthic organic matter (BOM) standing stock were also related to adjacent logging history. For example, fall standing stock of total benthic organic matter (TBOM) and course benthic organic matter (CBOM) were greater in study sites adjacent to forests that had not been logged for longer durations (Figs. 10a, P=0.011; and 10b, P=0.002, respectively). Additional significant relationships between adjacent logging and stream physical conditions were not detected (P>0.12).

Our estimates of logging history of the whole catchment were not significantly related to the study site macroinvertebrate variables measured in our analysis. We also did not detect relationships between predicted catchment groundwater velocity and our biological or physical measurements.

Relationships between macroinvertebrate communities and stream/riparian environment

Study sites that had a higher total GLEAS habitat index generally hosted greater mean yearly diversity of invertebrates (Fig. 11a, P=0.026) as well as greater Plecopteran biomass (Fig. 11c, P=0.006). Mean yearly Plecopteran density was also significantly related to total GLEAS score (R\(^2\) = 0.69, P = 0.04). We detected greater mean yearly Plecopteran biomass in study sites with greater canopy cover (Fig. 11d, P=0.048). Although greater mean yearly invertebrate
diversity also tended to be observed at study sites with more area in canopy (Fig. 11b, P=0.045),
there were nonlinearities in the relationship, with relatively high diversity at more open sites as well. Canopy cover over study sites was related to Plecopteran shredder biomass in early summer (Fig. 12a, P=0.005) and late summer (12b, P=0.004), and to shredder density in the early summer (Fig. 12c, P=0.014) and late summer (12d, P=0.016). Macroinvertebrates sampled in the fall showed no detectable linear relationships to reach or upstream canopy cover (P > 0.17).

There was however, a positive relationship between study site canopy cover and median substrate size in the study streams (Fig. 13, P=0.031). The density of shredders in late summer was greater in streams with more canopy cover (Fig. 14a, P=0.01) and the biomass of Plecopteran shredders tended to be greater in both early summer (Fig 14b, P=0.048) and late summer samples (Fig.14c, P=0.017). These streams with greater area of canopy cover in their upstream section also had lower mean daily water temperatures (Fig.15, P=0.009). Therefore, mean yearly Plecopteran taxa biomass was also negatively correlated with mean daily stream temperature (Fig. 16, P=0.04).

The dominance by *Tipula* biomass relative to the biomass of Plecopterans in the shredder functional group tended to be greater in streams with smaller substrate size (Fig. 17a, P=0.015) and greater percent fine sediment in riffles (Fig. 17b, P=0.002). This biomass dominance by *Tipula* also tended to be greater in study sites with lower canopy cover (Fig. 17c, P=0.019) and lower catchment slope (Fig. 17d, P=0.002). These relationships taken as a whole suggest that the shredder complex may vary in composition relative to the annual level of disturbance or coldwater habitat quality of the streams.

Course Benthic Organic Matter and TBOM in the fall were also both positively related to reach and mean upstream area in canopy cover (Fig. 18). Early and late summer Plecopteran shredder biomass was positively correlated with fall CBOM and TBOM (Fig. 19). Macroinvertebrate community variables as density were also found to be associated with BOM across study sites. Shredder densities in the early summer ($R^2 = 0.71$, $P = 0.03$) and late summer ($R^2 = 0.89$, $P = 0.001$) were positively correlated with fall CBOM. Fall TBOM standing stocks were positively correlated with late summer shredder densities (Fig. 20a) and yearly mean shredder densities were positively correlated with fall CBOM (Fig. 20b). Fall BOM variables were not correlated to any fall macroinvertebrate variables and summer BOM variables revealed no relationships with any seasonal or yearly macroinvertebrate variables.

In addition to the local reach scale relationships we detected, a number of macroinvertebrate, functional and taxonomic groups had significant, seasonal or yearly correlations with study site catchment area including yearly mean biomass of all invertebrates (Fig. 21a, P=0.004), gatherers (Fig. 21b, P=0.005), predators (Fig. 21c, P=0.026) and shredders (Fig. 21d, P=0.055). Catchment area also positively related to the densities of all total invertebrates (Fig. 22a, P=0.0003), predators (Fig. 22b, P=0.021), gatherers (Fig. 22c, P=0.004) and EPT taxa (Fig. 22d, P=0.0002).
DISCUSSION

The results of our comparative chronosequence study suggest a number of direct and possible indirect relationships between logging in adjacent forest stands and the physical and biological condition of riparian streams, thus supporting the broad predictions presented in Figure 1. However, we did not detect broad indicators of habitat disturbance or degradation in the form of detectable variation in, for example, the GLEAS habitat condition scores or widely used invertebrate metrics of disturbance such as EPT. Many of the members of EPT orders in our study streams were more taxa (e.g., Baetidae and Hydropsychidae) that are considered to be more tolerant of disturbance. Among the individual physical features of the stream habitat that appeared to respond to logging, both canopy cover and size of the stream substrate (see Fig. 2) were relatively reduced at sites within more recently logged forest stands. Although logging history of adjacent forest stands and mean daily water temperatures were not statistically related in this watershed, water temperature was significantly related to upstream canopy cover. Figure 3 describes this relationship as a result of disturbances sometimes attributed to logging practices and extends the prediction to indicate its influence on disturbance sensitive invertebrate taxa. The influence of these disturbances on the structure of biological communities forms the basis for the design and implementation of biomonitoring protocols (Fortino et al 2004). The effectiveness of biomonitoring therein depends on the principle that stream biota integrate physical and chemical disturbances through time and that the structure of stream communities at any given time reflect these disturbances (Karr 1999).

Although we did not detect broad (e.g., multimetric) indicators of stream disturbance in this study, we did detect multiple individual and likely interacting indicators of altered stream conditions. For example, Plecopteran biomass and Shannon diversity (taxonomic) of the stream invertebrate assemblage both appeared to be sensitive to stream habitat conditions, including canopy cover and general physical habitat quality. Plecopteran biomass was also correlated to mean daily stream temperature. Plecopteran taxa are key indicators of stream condition in many systems, especially headwater streams where the physical constraints of water temperature, substrate and riparian vegetation make the presence of Plecopteran taxa very dependent on local physical habitat (Stewart and Stark 2002). Because of these relationships, Plecopteran taxa have been used, either alone or in combination with Ephemeroptera and Trichoptera, as an effective indicator metric of local-scale conditions in biological monitoring programs (Wallace et al 1986, Wallace et al 1996). This suggests that Plecoptera taxa may be effective metrics for indicating the biological impacts of physical disturbances across our study sites yet no taxonomic (e.g., individual orders or EPT) or general functional group measured as biomass in this study were observed to directly relate to logging history in this watershed. However, direct and compelling associations were detected between stream invertebrates and physical stream conditions often attributed to land use practices (e.g., Figs. 2 and 3).

The use of patterns in community or habitat structure has been a common and often effective practice in stream monitoring procedures. The use of functional feeding group composition has also been used as an indirect metric with which to assess stream processes. Physical and trophic conditions in most streams are temporally dynamic and are often the result of disturbances distributed over a larger spatial and temporal scale (Harding et al 1998). In addition, concern has been raised that direct measures of variables implicated in stream ecosystem processes are lacking in monitoring programs (Gessner and Chauvet 2002). However, the issue remains that the choice of practical and effective direct measures of stream processes
can be difficult. The dependency of food webs in forested headwater streams on seasonal litter inputs (Cummins et al 1973) may present some practical metrics for the assessment of stream processes (see Figure 2). The strength of these interactions may offer a means for examining the possible influence of disturbances associated with logging practices on the nature of the relationship between patterns in community structure and stream ecosystem processes. The inclusion of benthic organic matter sampling in this study proved to be a key factor in understanding the possible influence of logging on stream function. A number of stream physical conditions have been shown to respond to watershed clear cutting including nutrient and organic matter dynamics and hydrological conditions (Likens and Borman 1995). Indeed, biological processing of organic matter is often implicated as being mechanistically involved in the linkage between forest disturbance and stream dynamics.

Logging history at our study sites was strongly related to both riparian canopy cover and fall benthic organic matter (BOM) standing stocks. The passage of organic matter though forested streams involves a dynamic balance between source and quality of input and the physical and biological factors influencing retention (Sedell et al 1978). Our results revealed a strong relationship between study site and upstream area in canopy cover and fall CBOM and TBOM standing stock. Other studies have found that physical retention of organic matter is a key mechanism determining streambed organic matter densities (Prochacka et al 1991) although certainly the supply rate of organic matter and its retention within the stream are both important mechanisms. We did not measure substrate conditions or flow conditions at the scale of individual organic matter samples, nor did we collect organic matter from woody debris dams, all of which have been shown to be important mechanisms influencing the retention of organic matter (Bilby and Likens 1980, Speaker et al 1984, Gurtz and Wallace 1984, Jones and Smock 1991, Doisey and Rabini 2001).

A number of studies have detected a strong relationship between shredder characteristics and BOM standing stock (Kirbey et al 1983, Wohl et al 1995) and processing rates (Cuffney and Wallace 1990). The physical processing of organic matter, primarily by the shredder functional group, has a critical role in the retention and transport of organic matter and ultimately the availability of nutrients to other members of the stream food web (Vannote et al 1980). We did not find a direct relationship between seasonal organic matter standing stock and its seasonally associated macroinvertebrate community; however, summer shredder density and Plecopteran shredder biomass were both strongly correlated with fall BOM standing stock. These variables of the shredder functional group were also the only macroinvertebrate community variables that were linearly related with watershed logging. Considering the importance of leaf litter inputs to headwater stream food webs and the seasonally pulsed nature of its supply to the stream communities throughout the year, the responses we detected in the shredder assemblage are likely to be expected. Food limitation has been shown to be a strong factor in stream community; biomass, secondary production and functional group composition in heterotrophic stream food webs (Richardson 1991, Dobson and Hildrew 1992, Wallace et al 1999). Fall leaf litter inputs may temporarily release resident stream communities from these trophic limitations; however, decreased BOM standing stocks over the winter and spring mediated through bioprocessing, hydrological and physical habitat conditions may have served as strong shaping factors of summer shredder communities. We sampled macroinvertebrates independently in riffles and not directly at the same points of BOM collection and as a result, our findings are limited to the stream reach scale. However, the strength of the relationship between BOM and
shredders across our sampling sites may imply that this is an effective scale at which to interpret local influences on ecosystem process in these streams.

One of the most surprising findings in this study was the relationship between the composition of the shredder functional group community and a number of key habitat variables. Total seasonal or yearly shredder biomass (all species combined) was not correlated to any of the habitat variables measured in our study and did not appear to be an effective measure of stream condition or organic matter dynamics. However the ratio of *Tipula* sp. to Plecoptera spp. within the shredder assemblage was negatively related to substrate size in riffles and positively related to percent fine sediment in riffles. *Tipula* sp. exhibit a number of behavioral and physiological traits that may help explain some of these relationships. *Tipula* sp. are relatively sensitive to organic pollution (Hilsenhoff 1987), but are highly tolerant of inorganic sedimentation (Relyea et al. 2000). All of the Plecopteran shredders sampled were intolerant of organic pollution (Hilsenhoff 1982) and although generic habitat preferences vary somewhat (Relyea et al. 2000), Plecoptera as a group are generally considered intolerant of inorganic sedimentation (Stewart and Stark 2002). Although we did not detect a significant relationship between substrate conditions and BOM standing stock, substrate size was one of the variables, along with canopy cover and fall TBOM and CPOM standing stocks that were significantly related to adjacent logging. Possibly as a result of life history or physiological traits, *Tipula* sp., has been shown to dominate shredder communities after catastrophic disturbances. Wallace et al (1986) found that after an insecticidal removal of invertebrates from a forested headwater stream, shredder biomass and organic matter bioprocessing recovered after two years; however, he found that *Tipula* sp. were twice as dominant in the treatment stream compared to abundances before treatment or in a nearby reference stream. There is also evidence that *Tipula* sp. may be able to take advantage of more refractory food sources not available to other shredders and as a result, persist in food limited systems such as may exist seasonally at our study sites (Barlocher 1983, Wallace et al 1999). The Trichoptera, *Lepidostoma* sp., which were a small fraction of shredder community biomass (1.6-2.9% seasonally), is also considered very tolerant of inorganic sediment (Relyea et al. 2000) and they displayed relationships to stream habitat similar to those of *Tipula* sp.

Strong relationships between watershed area and the biomass and density of gatherers, predators and total macroinvertebrates is consistent with the change in community structure along the longitudinal continuum in physical and trophic conditions described by Vannote et al (1980). The strength of these relationships in streams of standard stream order is surprising and may suggest a need to group study sites by a continuous measure such as watershed area. If longitudinal position in the watershed, measured as catchment area, is a predictor of community composition in these streams it did not appear to influence the seasonal or yearly distribution of BOM at the scale of stream reach across our study sites. Despite this, the relationship between leaf processing activities of shredders in headwater streams has been linked to nutrient availability of downstream detritivores (Short and Marsden 1977). Negative effects of logging on organic matter processes in headwater streams will certainly have a negative impact on patterns of macroinvertebrate community structure in downstream drainages.

**Conclusions**

- We detected no generalized relationships between the history of logging at the catchment or adjacent forest scale and study site general habitat condition as indicated by the GLEAS.
- Logging history at the catchment scale was not a significant predictor of study site biological or physical variables.
We found a significant relationship between adjacent logging history and Plecopteran taxa biomass and density. This result may favor the inclusion of Plecopteran taxa in biomonitoring indices created to measure local logging impacts.

Adjacent logging history was also significantly related to the canopy cover over a study site, substrate size and fall benthic organic matter standing stock.

Benthic organic matter standing stocks positively correlated with study site and upstream canopy cover, suggesting that local and upstream canopy is a strong determinant of organic matter dynamics at the local scale. Our failure to detect relationships between BOM standing stock and physical variables representing local retention may have been influenced by the techniques we used in the sampling and quantifying retention variables.

BOM standing stock maxima in the fall was positively related to the density and biomass of Plecopteran shredders and shredder density during BOM standing stock minimums in the summer, suggesting that organic matter availability may be constraining the summer shredder community, possibly through food limitation.

Food limitation and habitat alterations across our sites may have influenced the composition of shredder communities to favor Tipula sp., which possess traits allowing it more physical tolerance and physiological advantage in food utilization.

A number of functional group biomass and densities were correlated with watershed area even though our sites were all located in second-order streams. These relationships may indicate that communities are strongly linked with upstream processes across out sites. Reach-scale organic matter distribution was not related to watershed area.

BOM standing stock sampling may be a practical and effective means of measuring the influence local logging practices logging on organic matter dynamics, a critical ecological process in forested headwater streams.

Our results suggest that alteration to land and forest stands adjacent to headwater streams caused by logging practices may be causing a shift in local stream communities toward one with a greater proportion of more tolerant taxa and reduced local benthic organic matter standing stocks to the extent that organic matter may limit the presence of species dependent on the seasonal input and retention of fall leaf litter (i.e. shredders). Relationships between several macroinvertebrate functional groups and watershed area may reflect a strong relationship between local community structure and upstream processes, suggesting that alteration in local organic matter dynamics may be influencing ecosystem processes and community structure at a much larger scale. The extent of alteration to aquatic ecosystems by selection logging in forested watersheds in the northern hardwood ecosystem is uncertain. Our results suggest that the effects of present logging techniques may have created a measurable change in ecosystem process and community structure at the local scale across streams in the Otter River Watershed.
LITERATURE CITED


MDEQb. 2002. Great Lakes and Environmental Assessment Section Procedure #51, Qualitative Biological and Habitat Survey Protocols For Wadable Streams and Rivers. MI DEQ, Surface Water Quality Division, GLEAS.


Table 1. Study stream site names, catchment area and slope, and the number of years since the most recent selection logging of adjacent forest stands and of the catchment (mean value across stands within catchment) of the study site had occurred.

<table>
<thead>
<tr>
<th>Stream name</th>
<th>Stream code</th>
<th>Catchment area (km²)</th>
<th>Mean percent catchment slope</th>
<th>Years post adjacent forest logging</th>
<th>Mean years post catchment logging</th>
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</thead>
<tbody>
<tr>
<td>Small Bear Creek</td>
<td>SMB1</td>
<td>5.02</td>
<td>10.2</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Tributary West Branch</td>
<td>OSR1</td>
<td>14.56</td>
<td>6.1</td>
<td>3</td>
<td>6</td>
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<tr>
<td>Bart Creek</td>
<td>BTC1</td>
<td>3.36</td>
<td>17.9</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>South Branch Bear Creek</td>
<td>SBR2</td>
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<td>11</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Beaver Creek</td>
<td>BEC1</td>
<td>9.36</td>
<td>10.6</td>
<td>5</td>
<td>8</td>
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<tr>
<td>Lake Fifteen Creek</td>
<td>LKF1</td>
<td>5.38</td>
<td>6.4</td>
<td>9</td>
<td>13</td>
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<td>North Branch Bear Creek</td>
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<td>12.66</td>
<td>13.9</td>
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<td>9</td>
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<tr>
<td>Thirteenmile Creek</td>
<td>THM1</td>
<td>10.03</td>
<td>13.1</td>
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<td>8</td>
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<tr>
<td>West Branch Sante River</td>
<td>WBS1</td>
<td>8.29</td>
<td>15.6</td>
<td>11</td>
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Table 2. Habitat measurements conducted at the local reach (study site), upstream and catchment scales.

<table>
<thead>
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<th>Variable</th>
<th>Reach</th>
<th>Upstream</th>
<th>Catchment</th>
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</thead>
<tbody>
<tr>
<td>Macroinvertebrate</td>
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<td>●</td>
<td>●</td>
</tr>
<tr>
<td>Benthic organic matter</td>
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<td></td>
</tr>
<tr>
<td>GLEAS</td>
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<td>●</td>
<td></td>
</tr>
<tr>
<td>Median substrate size</td>
<td>●</td>
<td>●</td>
<td></td>
</tr>
<tr>
<td>Water Temperature</td>
<td>●</td>
<td>●</td>
<td></td>
</tr>
<tr>
<td>Median discharge</td>
<td>●</td>
<td>●</td>
<td></td>
</tr>
<tr>
<td>Stream slope</td>
<td>●</td>
<td>●</td>
<td></td>
</tr>
<tr>
<td>Woody debris</td>
<td>●</td>
<td>●</td>
<td></td>
</tr>
<tr>
<td>Channel geomorphic unit</td>
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<td>●</td>
<td></td>
</tr>
<tr>
<td>Canopy cover area</td>
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<td>●</td>
<td></td>
</tr>
<tr>
<td>Forest years since logged</td>
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<td>●</td>
<td>●</td>
</tr>
<tr>
<td>Catchment area</td>
<td></td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>Catchment slope</td>
<td></td>
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<td>●</td>
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</tbody>
</table>
**FIGURE LEGENDS**

Figure 1. Predicted general associations between watershed land use and condition, stream environment, resource input and aquatic invertebrate communities in a hypothetical watershed.

Figure 2. Potential relationships among logging and stream organic matter dynamics as they relate to the composition of stream macroinvertebrates based on functional groupings (e.g., shredders, collectors and predators).

Figure 3. Potential relationships among logging, riparian canopy, erosional processes in the watershed and stream habitat with respect to their effects on aquatic invertebrates that are sensitive to disturbance.

Figure 4. Map of Otter River watershed study sites and catchments.

Figure 5. Mean abundance (± 1 standard deviation) of selected macroinvertebrate taxonomic groups across sampling sites, seasons and years by a) Biomass and b) Density.

Figure 6. Mean abundance (± 1 standard deviation) of selected macroinvertebrate functional groups across sampling sites, seasons and years by a) Biomass and b) Density.

Figure 7. Yearly mean distribution of benthic organic matter (BOM) standing stock across study sites and channel units.

Figure 8. Relationship between years since adjacent forest stands were most recently logged and a) Summer shredder density and b) Summer Plecopteran shredder biomass.

Figure 9. Years since adjacent forest stands were most recently logged and a) Study site median substrate size and b) Study site area in canopy cover.

Figure 10. Relationship between the number of years since adjacent forest stands were most recently logged and a) Fall mean total benthic organic matter (TBOM) standing stock and b) Fall mean course benthic organic matter (CBOM) standing stock.

Figure 11. Relationship between total GLEAS habitat index score and a) mean yearly Shannon diversity and c) Plecopteran taxa biomass. Relationship between the area of canopy cover at study sites and the b) Shannon diversity of invertebrate taxa based on biomass and d) Plecopteran taxa biomass.

Figure 12. Relationship between the area of canopy cover at study sites and a) Early summer Plecopteran shredder biomass, b) Late summer Plecopteran shredder biomass, c) Early summer shredder density and d) Late summer shredder density.

Figure 13. Relationship between the area of canopy cover at study sites and median stream substrate size.
Figure 14. Relationship between upstream (1km) canopy cover area and a) Late summer shredder density, b) Early summer Plecopteran shredder biomass and c) Late summer Plecopteran shredder biomass.

Figure 15. Relationship between upstream canopy cover area and mean daily stream temperature at the study sites.

Figure 16. Relationship between mean daily stream temperature at study sites and mean yearly Plecopteran biomass.

Figure 17. Relationship between the ratio of *Tipula* spp. to Plecoptera spp. biomass and a) Median substrate size in study site riffles, b) percent fine sediment in study site riffles, c) Study site canopy cover area and d) Catchment slope.

Figure 18. Relationship between study site canopy cover area and a) Fall mean course benthic organic matter (CBOM) standing stock and b) Fall mean total benthic organic matter (TBOM) standing stock. Upstream (1km) canopy cover area and its correlation with c) Fall mean CBOM standing stock and d) Fall mean TBOM standing stock.

Figure 19. Relationship between fall mean total organic matter standing stock (TBOM) and a) Early summer Plecopteran shredder biomass and c) Late summer Plecopteran shredder biomass. Relationship between fall mean course benthic organic matter (CBOM) and b) Early summer Plecopteran shredder biomass and d) Late summer Plecopteran shredder biomass.

Figure 20. Relationships between a) fall mean total benthic organic matter (TBOM) standing stock and summer shredder density, and b) fall mean course benthic organic matter (CBOM) and mean yearly shredder density.

Figure 21. Relationship between catchment area above study sites and yearly mean biomass of a) Total invertebrates, b) Gatherers (note different scale), c) Predators and d) Shredders.

Figure 22. Relationship between catchment area upstream of study sites and yearly mean density of a) Total invertebrates, b) Predators (note different scale), c) Gatherers and d) EPT taxa.
Figure 1

Watershed Condition and Land use

Stream Environment

Resource Supply

Aquatic Macroinvertebrates
Figure 2

Logging

Riparian Forest Canopy

Benthic Organic Matter

Sedimentation (sand loading)

Shredders

Predators

Collectors

Downstream transport of Organic Matter

(-) reduced retention

(+)(-) reduced retention

(+)(-) reduced retention

(+)(-) reduced retention

(+)(-) reduced retention

(+)(-) reduced retention

(+)(-) reduced retention
Logging and Road Building

Riparian Canopy

Water Temperature

Erosion and Runoff

Disturbance Sensitive Taxa

(+)

(-)

(-)

(-)

(-)

(+)

(-)
Figure 5

**a)**

Density (individuals/m²)

- Odonata
- Diptera
- Trichoptera
- Ephemeroptera
- Plecoptera
- Coleoptera
- EPT

**b)**

Biomass (g/m²)

- Odonata
- Diptera
- Trichoptera
- Ephemeroptera
- Plecoptera
- Coleoptera
- EPT

Taxonomic order

- Spring
- Summer
- Fall
Figure 7

(a) AFDM (g m$^{-2}$) for CBOM, FBOM, and TOM during summer and fall.

(b) AFDM (g m$^{-2}$) for different habitats (Pool, Riffle, Run) during summer and fall.
Figure 8

a) Summer shredder density (individuals m\(^{-2}\)) over years post logging. The regression line has an $r^2 = 0.681$ and $P = 0.044$.

b) Summer Plecoptera shredder biomass (g m\(^{-2}\)) over years post logging. The regression line has an $r^2 = 0.773$ and $P = 0.015$. 
Figure 9

(a) Reach median substrate size (mm)

\[ r^2 = 0.655 \]
\[ P = 0.055 \]

(b) Study site canopy cover (m²)

\[ r^2 = 0.733 \]
\[ P = 0.025 \]
Figure 10

a) $r^2=0.793$  
$P=0.011$

b) $r^2=0.882$  
$P=0.002$
Figure 11

Shannon diversity ($H^*$)

Total GLEAS habitat value

Study site canopy cover ($m^2$)

Plecopteran Biomass ($g*m^{-2}$)

r$^2=0.728$
P=0.026

r$^2=0.680$
P=0.045

r$^2=0.829$
P=0.006

r$^2=0.671$
P=0.048
Figure 13

Study site canopy cover (m²)

Reach Median substrate size (mm)

$r^2 = 0.713$

$P = 0.031$
Figure 14

(a) Shredder density (individuals m\(^{-2}\)) vs. upstream canopy cover (m\(^2\)).

(b) Plecoptera shredder biomass (g m\(^{-2}\)) vs. upstream canopy cover (m\(^2\)).

(c) Plecoptera shredder biomass (g m\(^{-2}\)) vs. upstream canopy cover (m\(^2\)).

- \(r^2 = 0.76\)
- \(P = 0.01\)

- \(r^2 = 0.670\)
- \(P = 0.048\)

- \(r^2 = 0.761\)
- \(P = 0.017\)
Figure 15

Mean daily temperature (°C) vs. Upstream canopy cover (m²)

$r^2 = -0.803$
$P = 0.009$
Figure 16

Mean yearly Plecopteran Biomass (g/m²) vs. Mean daily temperature (°C)

- $r^2 = 0.70$
- $P = 0.04$
Figure 17

- Median substrate size in riffles (mm)
  - $r^2 = 0.773$
  - $p = 0.015$

- Percent fine sediment in riffles
  - $r^2 = 0.880$
  - $p = 0.002$

- Tipula: Plecopteran shredder biomass (g/m²)
  - $r^2 = 0.773$
  - $p = 0.019$

- Watershed slope
  - $r^2 = 0.872$
  - $p = 0.002$
Figure 18

(a) \( r^2 = 0.860 \)
\( P = 0.003 \)

(b) \( r^2 = 0.883 \)
\( P = 0.002 \)

(c) \( r^2 = 0.896 \)
\( P = 0.001 \)

(d) \( r^2 = 0.911 \)
\( P = 0.0006 \)
Figure 19

- **a)**: $r^2 = 0.789$, $P = 0.011$
- **b)**: $r^2 = 0.719$, $P = 0.029$
- **c)**: $r^2 = 0.796$, $P = 0.010$
- **d)**: $r^2 = 0.898$, $P = 0.001$
Figure 20

a) Shredder density (individuals m\(^{-2}\)) vs. Fall TBOM AFDM (g m\(^{-2}\))

- \(r^2 = 0.780\)
- \(P = 0.013\)

b) Shredder density (individuals m\(^{-2}\)) vs. Fall CPOM AFDM (g m\(^{-2}\))

- \(r^2 = 0.703\)
- \(P = 0.035\)
Figure 21

(a) $r^2 = 0.849$, $P = 0.004$

(b) $r^2 = 0.831$, $P = 0.005$

(c) $r^2 = 0.730$, $P = 0.026$

(d) $r^2 = 0.655$, $P = 0.055$
Figure 22

Density (individuals/m²) vs. Catchment area (km²)

- a) $r^2 = 0.929$, $P = 0.0003$
- b) $r^2 = 0.745$, $P = 0.021$
- c) $r^2 = 0.851$, $P = 0.004$
- d) $r^2 = 0.941$, $P = 0.0002$
Appendix A. Taxa list from sampling reaches in the Otter River watershed

Annelida
  Hirudinea
  Oligochaeta

Arthropoda
  Arachnida
    Acari
      Hydrachnidae
        Hydracarina sp.

Insecta
  Coleoptera
    Curculionidae
      Listronotus sp.
    Dryopidae
      Helichus sp.
    Dytiscidae
      Agabus sp.
      Unidentified genus
    Elmidae
      Optioservus sp.
  Collembola
    Unidentified genus
  Diptera
    Athericidae
      Atherix sp.
    Ceratopogonidae
      Atrichopogon sp.
      Unidentified genus
      Dasyhelea sp.
    Chironomidae
      Unidentified genus (Tanypodinae removed)
    Tanypodinae
      Unidentified genus
    Dixidae
      Dixa sp.
    Empididae
      Chelifera sp.
      Clinocera sp.
      Hemerodromia sp.
    Muscidae
      Unidentified genus
    Psychodidae
      Pericoma sp.
    Simuliidae
      Simulium sp.
Stratiomyidae
  *Stratiomyris sp.*

Tabanidae
  *Chrysops sp.*
  *Hybomitra sp.*

Tipulidae
  *Antocha* sp
  *Dicranota sp.*
  *Erioptera sp.*
  *Hesperoconopa sp.*
  *Limnophila sp.*
  *Limonia sp.*
  *Pedicia sp.*
  *Pilaria sp.*
  *Prinocera sp.*
  *Pseudolimnophila sp.*
  *Tipula sp.*
  Unidentified genus.

Ephemeroptera
  Baetidae
    *Acentrella sp.*
    *Baetis sp.*
  Ephemerellidae
    *Drunella sp.*
    *Ephemerella sp.*
    *Serratella sp.*
  Ephemeridae
    *Hexagenia sp.*
  Heptageniidae
    *Epeorus sp.*
    *Heptagenia sp.*
    *Rhithrogena sp.*
    *Stenonema sp.*
  Leptophlebiidae
    *Paraleptophlebia sp.*
  Trichorythidae
    *Tricorythodes sp.*

Hemiptera
  Belostomatidae
    *Belostoma sp.*
  Gerridae
    Unidentified genus

Lepidoptera
  Pyralidae
    Unidentified genus

Megaloptera
Sialidae
   *Sialis sp.*

Odonata
   Unidentified genus

Aeshnidae
   Unidentified genus
   *Boyeria sp.*

Coenagrionidae
   *Argia sp*
   *Nehalennia sp.*

Cordulegastridae
   *Cordulegaster sp.*

Gomphidae
   *Ophiogomphus sp.*

Plecoptera

Capniidae
   *Allocapnia sp.*
   *Paracapnia sp.*

Chloroperlidae
   *Haploperla sp.*

Leuctridae
   *Leuctra sp.*

Nemouridae
   *Amphinemura sp.*

Perlidae
   *Acroneuria sp.*

Perlodidae
   *Clioperla sp.*
   *Isogenoides sp.*
   *Isoperla sp.*
   Unidentified genus

Taeniopterygidae
   *Taeniopteryx sp.*

Trichoptera
   Unidentified genus

Brachycentridae
   *Brachycentrus sp.*
   *Micrasema sp.*

Glossosomatidae
   *Agapetus sp.*
   *Glossosoma sp.*
   *Protoptila sp.*

Hydropsychidae
   *Arctopsyche sp.*
   *Ceratopsyche sp.*
   *Cheumatopsyche sp.*
Diplectrona sp.
Hydropsyche sp.
Unidentified genus
Parapsyche sp.

Hydroptilidae
Hydroptila sp.
Oxyethira sp.
Stactobiella sp.

Lepidostomatidae
Lepidostoma sp.

Leptoceridae
Mystacides sp.
Oecetis sp.
Triaenodes sp.

Limnephilidae
Goera sp.
Hesperophylax sp.
Hydatophylax sp.
Limnephilus sp.
Neophylax sp.
Platycentropus sp.
Psychoglypha sp.

Molannidae
Molanna sp.

Philopotamidae
Chimarra sp.
Dolophilodes sp.
Unidentified genus

Polycentropodidae
Cernotina sp.

Rhyacophilidae
Rhyacophila sp.

Mollusca
Gastropoda
Limnophila
Ancyliidae
Ferrissia sp.
Lymnaeidae
Fossaria sp.
Physidae
Physella sp.
Planorbidae
Unidentified genus

Pelecypoda
Veneroida
Sphaeriidae
*Pisidium sp.*  
*Sphaerium sp.*  

Nematoda

Unidentified genus

Nematode

Adenophohorea

Mermithida

Mermithidae

Unidentified genus

Nematomorpha

Unidentified genus

Platyhelminthes

Turbellaria

Neorhabdocoela

Typhloplanidae

*Opistomum sp.*