

**Sources of small-scale variation in headwater stream habitat
and macroinvertebrate communities**

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In partial fulfillment of the requirements of the degree of Master of Science

Lakehead University, Department of Biology
2009

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ABSTRACT

The extent to which small stream habitats and communities are influenced by the surrounding terrestrial environment is a function of the linkage between aquatic and terrestrial systems. The strength of that linkage is mediated primarily by topography and can affect the susceptibility of the stream to impairment by harvesting disturbance. Stream habitat and macroinvertebrate communities were studied at 30 small stream sites to characterize their associations with the surrounding terrestrial environment at the riparian and catchment scales. Local topography was described using the 'reach contributing area' (RCA) as a measure of the lateral terrestrial area contributing to the stream reach. In the first section of the study I examined the linkage between stream habitat characteristics and riparian and catchment scale terrestrial variables in light of differences in local topography, and assessed the effects of harvesting disturbance on stream habitat as mediated by that aquatic-terrestrial linkage. Using redundancy analysis (RDA) riparian scale factors were found to be more strongly correlated with local habitat variability than catchment scale factors in both small and large RCAs, and in both reference and harvested sites. In sites with large RCAs riparian scale variables explained 40% more variation than catchment scale variables. Aquatic habitat at sites with recent local harvesting had significantly higher temperatures and nitrogen concentrations (MANOVA $p < 0.05$). Stream habitat variation in harvested sites was more strongly correlated with forest cover, whereas variation in reference sites was more strongly correlated with topographic variables. In the second section I characterized how macroinvertebrate communities are structured based on aquatic and terrestrial variables at 3 spatial scales, and how those influences differ based on local topography. The effects of harvesting on macroinvertebrate community structure were also examined in the final section. Local scale variables explained the most variation in taxonomic and functional invertebrate community structure (51.6% and 59.1%), followed by catchment scale variables (43.9% and 43.5%). In large RCA sites, the riparian scale variables had almost 10% more influence on taxonomic structure than catchment scale variables, and in small RCA sites catchment scale variables explained almost 23% more variation in feeding guild structure than riparian scale variables. The total abundance and richness of macroinvertebrates was significantly higher in harvested sites than in reference sites (ANOVA $p < 0.05$), and communities differed significantly in structure (MRPP $p < 0.05$). This study shows the effect of local topography on the linkage between aquatic and terrestrial environments. The RCA effect combined with the effects of harvesting disturbance on small streams can be combined to better understand processes driving variability in small stream habitats and communities. This understanding can then be applied to management practices to better conserve all aspects of headwater stream environments.

ACKNOWLEDGEMENTS

Many people contributed to my success in completing this thesis and I would like to gratefully acknowledge them. It has been a great pleasure to work with my supervisor Rob Mackereth, and I would like to thank him for accepting me into his lab (without ever meeting me!) and for always having time when I burst into his office with a million questions about stats. With his help I have gained the skills and confidence in my abilities as a researcher that will get me through the next steps in my career.

Thank you to the whole CAEP lab! Darren McCormick is responsible for all of the GIS analysis and modelling that was used in this thesis. Without him I would not have had a project (and far fewer graphics for presentations!). Bruce Thacker was invaluable in helping me find my feet in my one field season and kept everything running smoothly so that I could focus on collecting my data. Hayley Veldhoen was fantastic company in the lab and a great help with invert ID, which kept me sane after 3 months at the microscope. I'd like to thank my fellow students who have also become great friends. Lisa McKee has been an amazing source of energy and moral support in the lab and for months out in the Nipigon Forest, and Eric Misener has been great support in the lab and on coffee runs, patiently listening to my diatribes about methodology and statistics. Thanks also to my field crew out in Nipigon, Victoria Danco, Emma Loud, and Craig Wilson for all their hard work.

Thank you to my committee members, Joe Carney and Azim Mallik, for constant streams of literature sent my way and for constructive comments both during the development phase and on the final thesis.

Funding from the Ontario Ministry of Resources through the Canada-Ontario Agreement Respecting the Great Lakes Basin Ecosystem and the Applied Research and Development Branch, and from the Ontario Graduate Scholarship program, and Lakehead University is gratefully acknowledged here as well.

Thank you to all for making my time here at CNFER valuable and enjoyable!

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1.0 GENERAL

1.1 GENERAL INTRODUCTION

Headwater streams are ecologically significant because of their unique habitat and the ecological services they provide to the downstream environments. The close interface between aquatic and terrestrial environments creates a unique and diverse habitat which supports biological communities necessary for the ecological functioning of the headwaters and downstream reaches. Headwater streams show the maximum interface with the terrestrial environment (Vannote et al. 1980). By modeling hillslope and riparian relationships for a river system, McGlynn and Seibert (2003) found that 85% of the total catchment area was contributing to streams with a local catchment of less than 20ha. This close relationship between small streams and the terrestrial environment means that variations in terrestrial factors anywhere within the catchment are likely to influence instream habitat characteristics and the benthic macroinvertebrate communities therein. Understanding which factors drive those relationships is important for characterizing small scale stream variability and the potential impacts of disturbance within the catchment.

Sources of variability in stream conditions can be longitudinal (relating to the larger catchment scale) or lateral (relating to riparian variables and local land use). Findings by Corkum (1989) and Challen (2002) that variation in benthic invertebrate communities was most closely associated with ecological region and total catchment size suggest a dominant longitudinal effect. The River Continuum Concept (Vannote et al. 1980) characterizes longitudinal variability by hypothesizing that communities will follow

predictable patterns along a downstream gradient from small headwater streams to large rivers. This theory emphasizes the longitudinal contributions of stream basins including characteristics upstream of the site such as catchment use, amount of stream flow, and upstream inputs of resources or pollutants. Bouchard and Boisclair (2008) examined the role of local, longitudinal and lateral variables on stream fish habitat and found that only local and longitudinal variables significantly contributed to the model. What is known about stream habitats and communities is largely from observation of natural longitudinal factors (stream size, catchment area) or by experimental manipulation or disturbance of lateral factors (logging of riparian buffer strips). Studies on natural variation of lateral inputs related to stream communities are lacking.

Lateral impacts on stream habitat include inputs from adjacent terrestrial environments and occur on a smaller spatial scale than longitudinal factors. Lateral inputs to the stream include water, nutrients, and organic matter contributed by upland and riparian areas, excluding those inputs contributed by flow from upstream. These lateral inputs are influenced by the riparian zone which can be defined as a three-dimensional zone of direct interaction between the terrestrial and aquatic ecosystems (Gregory et al. 1991). The riparian zone carries out several ecological functions that affect the local stream habitat including deposition of organic and inorganic material, providing varied in-stream habitats with respect to vegetation and shade, and affecting the abundance and quality of nutrients entering the stream (Gregory et al. 1991).

Ultimately, stream habitats are structured by a combination of large scale watershed characteristics, smaller scale lateral characteristics and the biotic community living within the habitat. Frissell et al. (1986) put forth a hierarchical model for stream classification based on the concept that variables at a smaller spatial scale are being constrained by characteristics at a larger scale. The River Continuum Concept is a good starting point as a model for large scale longitudinal variability but more needs to be understood about the heterogeneity of lateral and local in-stream factors within that framework (Fausch et al. 2002). Resolving the association between variables at these different spatial scales, local habitats and biotic communities, and how harvesting disturbance may influence this association is important for developing conservation strategies. Several studies have investigated the influence of variables at multiple spatial scales (local habitat, intermediate “riparian” scale variables, catchment scale variables, and ecoregion or “mega” scale variables) on in-stream characteristics and communities (Sponseller et al. 2001; Weigel et al. 2003; Feld and Hering 2007) with varying results. Most studies agree, however, that variation in local habitat characteristics or biotic communities can only be explained using a combination of variables at multiple spatial scales.

The influence of terrestrial characteristics at different spatial scales on local stream habitat factors depends on the connectivity in the landscape, which can be driven primarily by topography (Montgomery 1999). Groundwater flowpaths, for example, can be predicted by surface topography when permeable sediments are relatively shallow (McGlynn and Seibert 2002). Topography can influence the flux and direction of

groundwater flow as it will increase with steeper hillslopes and will always flow in the direction of the steepest gradient (Vidon and Hill 2006). Nitrogen flux, which can be limiting to production and highly variable in streams, is controlled by soil conditions and topography. Flux is increased with steeper hillslopes and decreased with longer residence time in the soil due to immobilization by plants and microbial communities (Vidon and Hill 2004). Topographic convergence focuses surface and subsurface flows (Montgomery 1999), which may therefore generate greater fluxes of groundwater and nutrients into certain stream reaches. In this study I define topographic convergence as the “reach contributing area” (RCA) which is the area of land lateral to a stream reach contributing only to that reach (Theobald et al. 2006).

McGlynn and Seibert (2003) state that in areas dominated by bedrock and shallow soil, the dynamics of hillslope and riparian inputs to a stream will be determined by topography. The concept of reach contributing area (RCA) is a relatively new method of characterizing natural lateral variation. Natural changes in the topography and geology of the surrounding landscape will create variation in the RCA of stream reaches at a relatively small scale, which can affect riparian and in-stream habitat characteristics. The RCA encompasses many intermediate scale variables that can affect in-stream habitat and local conditions, such as vegetation and forest communities, geological forms, topographic relief and soils. A larger RCA will naturally have more vegetation, greater potential for generating surface or subsurface flow, and greater variation in topography than a very small RCA. Stream reaches with a large RCA may then show a stronger association with those lateral variables than one with a small RCA, which would have a

relatively stronger association with longitudinal or catchment scale variables. The size of the RCA may determine the strength of correlation between local stream habitat and either intermediate or “riparian” scale landscape variables and large or “catchment” scale landscape variables. A stronger correlation with lateral, riparian scale variables may then influence the magnitude of response to harvesting disturbance through tighter linkages with the harvested area.

These small scale differences in terrestrial linkages and instream habitat characteristics, could potentially influence biotic aquatic communities on a much smaller scale than has been previously studied (historically comparisons between catchment areas, or between streams using approximately 50-200m reaches). Understanding how these small scale differences in the reach contributing area affect the diversity and composition of aquatic communities can elucidate patterns in processes such as nutrient cycling and organic decomposition which are the basis for the functioning of the larger stream and river system (Vannote et al. 1980). This study has implications for improving the use of aquatic invertebrates as indicators of habitat impairment and for forest management practices involving guidelines for buffer strips along streams. Using invertebrate communities to reflect differences on a small scale can also provide useful guidelines for how sensitive these communities are, and how well they are able to reflect differences in local, riparian, and catchment characteristics.

This study has 2 main components. The first component is to characterize the linkage between local stream habitat characteristics and the intermediate (or “riparian”) scale, and

catchment scale environmental factors surrounding it. The contributions of each spatial scale, and variables within those scales, to explain the variation in local habitat characteristics are determined and compared between sites with small RCAs and large RCAs. The effect of forest harvesting in light of that linkage is determined by comparing the local characteristics at harvested and reference sites and the variables at the riparian and catchment scales most correlated with those characteristics.

The second component is to characterize the linkage of benthic macroinvertebrate community assemblages with stream habitat, riparian, and catchment scale characteristics. The relative contributions of each spatial scale to explain variation in both taxonomic and functional feeding guild assemblages is determined and compared between sites with small RCAs and large RCAs. Harvesting effects are examined by comparing communities in reference and harvested stream sites. The potential for a difference in response to harvesting between small RCA sites and large RCA sites can be inferred from the results.

1.2 GENERAL METHODS

1.2.1 Study area

Streams were studied in the Nipigon Bay watershed on the North shore of Lake Superior, approximately 100km East of Thunder Bay, Ontario (Fig 1). Sites were spread over 7 sub-watersheds (Jackfish, Jackpine, Gravel, Cypress, Ozone, Dublin and Recover) which are in the Lake St. Joseph Plains and Superior Highlands Plains ecoregions (Wickware and Rubec 1989). Both ecoregions are dominated by granitic bedrock covered with

shallow sandy to loamy moraine. Average yearly temperature in the area is 1.7° C, with an average rainfall of 576.6 mm and an average snowfall of 237.5 cm. Forest cover is dominated by *Picea mariana* (Black Spruce) with some *Picea glauca* (White Spruce), *Abies balsamea* (Balsam Fir), *Pinus banksiana* (Jack Pine), *Betula papyrifera* (White Birch), *Populus tremuloides* (Trembling Aspen), and *Acer spicatum* (Mountain Maple) stands. The main land use in the area is forest management.

1.2.2 Site selection

All sites were selected on streams with a 1 km² (+/- 30%) catchment area. Using the Ontario provincial 20 m resolution digital elevation model (Ontario Ministry of Natural Resources 2005), a model was constructed using a GIS to delineate reach contributing areas (RCA), excluding contributions from upstream, for all the streams of interest (ArcGIS, ArcMap version 9.2, ESRI Inc., Redlands, CA). RCAs were delineated for each 20 m cell of the model. Sites were selected having a reach contributing area of less than 800 sq. m (0.08 ha) for the “small RCA” class and greater than 10 ha for the “large RCA” class. Sites were located from the center of the 20 m model cell. If 2 sites were located on the same stream, the large RCA site was at least 200 m downstream of the small RCA to reduce confounding effects of large upstream lateral inputs persisting into the small RCA sites and of movement of invertebrates between sites. Local topography was confirmed visually before accepting a study site. Sites were selected in both reference (unharvested) and harvested areas. Harvested sites had been clear-cut adjacent to the stream between 1 to 6 years previously and showed very little regrowth of forest

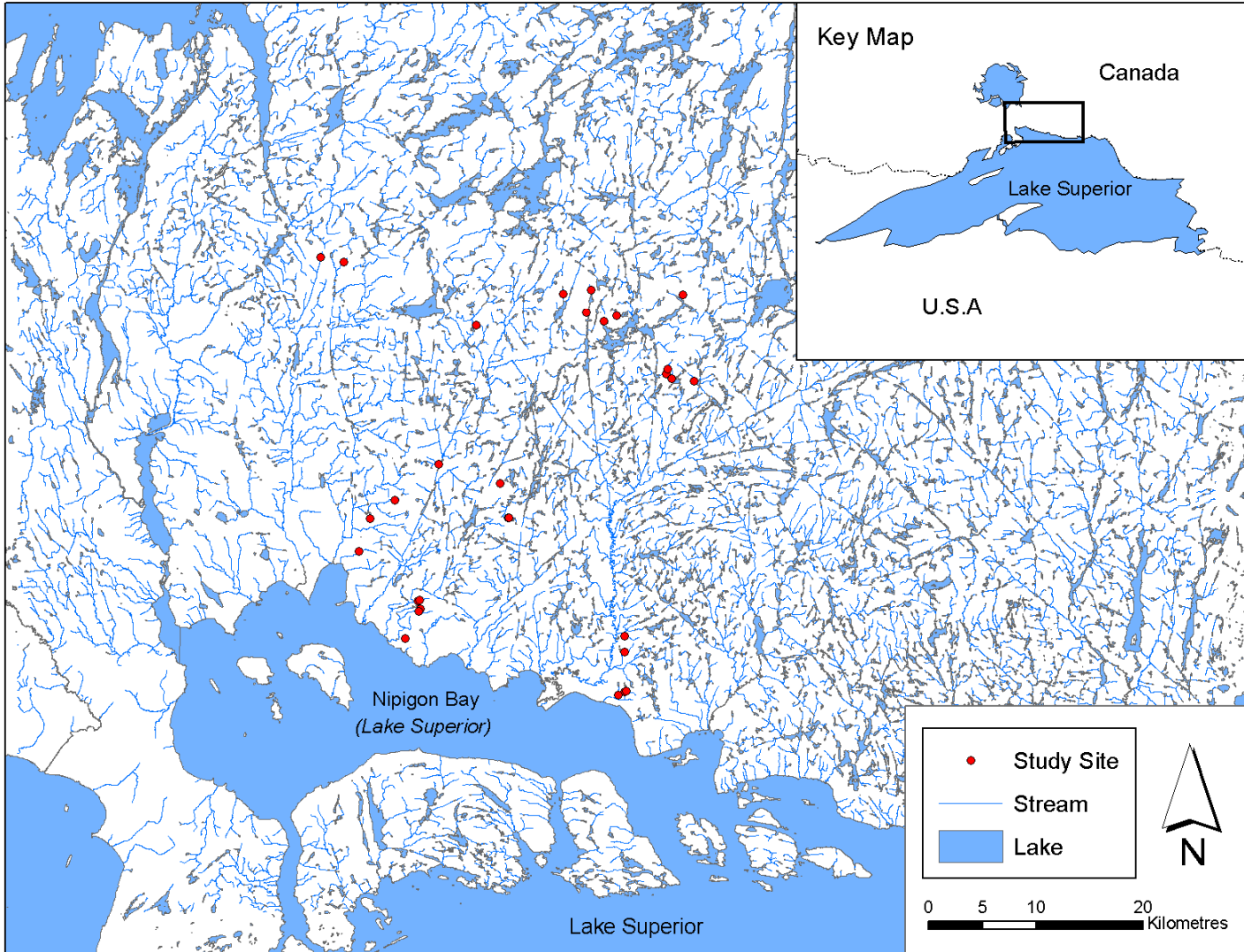


Figure 1. Map of study area and study sites used in this study

(trees were sparse and <1.5 m in height). All harvested streams had treed buffers between 30-50 m in width.

Twenty-three sites were selected in reference (unharvested) areas of which 12 had small RCAs and 11 had large RCAs. Seven sites were selected in harvested areas of which 3 had small RCAs and 4 had large RCAs.

1.2.3 Stream habitat

Study reaches were 10 m in length, entirely contained within the 20 m cell of the GIS model for which the RCA was delineated, which allowed me to study immediate local effects of large lateral inputs. In-stream habitat variables were all measured during summer stream base-flow conditions in July of 2008. The gradient of each stream reach was measured with a clinometer. Canopy cover was measured with a densiometer from the middle of the channel at the top and bottom of each reach. Streams were sufficiently narrow that separate canopy measurements were not required for each side of the stream. Stream wetted width, bankfull width, bank height and maximum depth were measured at the top, middle, and bottom of each reach. Detritus and woody debris were recorded in the categories absent (0), present (1) or abundant (2) at 3 locations for a total score out of 6. Substrate was quantified by measuring the median axis of 50 particles selected at random along the entire length of the reach. Substrate particles were sorted into classes based on a modification of the Wentworth scale (Wentworth 1922): bedrock (>999 mm), boulder (301-999 mm), cobble (51-300 mm), pebble (21-50 mm), gravel (1-20 mm), sand, and silt. The variable “% fine sediment” was calculated as the percent of all

substrate that was sand or silt. Discharge was measured at one transect in each reach using a Flo-Mate Model 2000 portable flow meter (Marsh-McBirney, Inc, Frederick, MD, USA). Temperature, pH, dissolved oxygen (DO), conductivity and total dissolved solids were measured with a YSI 600 QS probe (YSI incorporated, Yellow Springs, OH, USA). Water samples were collected once at the time of stream surveys, and sent to the Lakehead University Center for Analytical Services (LUCAS) for total nitrogen and total phosphorus analysis.

To estimate primary production, periphyton samples were collected by scraping off a known surface area of a rock from the stream or, in the absence of large substrate particles, a sample of substrate of that same surface area was collected. Samples were rinsed into an opaque container and frozen following the USEPA rapid bioassessment protocols (Barbour et al. 1999). Periphyton samples were later thawed and filtered through glass fibre filters with a 0.7 μm pore size for chlorophyll *a*, and ash-free dry mass analysis at LUCAS following the USDA Forest Service protocols (Davis et al. 2001).

1.2.4 Riparian scale assessment

The RCA of each stream reach was calculated in a GIS using a digital elevation model. All “riparian scale” characteristics include all terrestrial area within the RCA, including any upland area not included in the true wetland riparian zone. The riparian zone edge was determined as a distinct change from riparian wetland vegetation or a distinct change in slope. Width and slope of the zone was measured on both banks at the top and bottom of each reach. Stem density of trees was also measured within the RCA using the point-

centered quarter method (Barbour et al. 1987) along transects of 50-100 m perpendicular to the stream beginning at the riparian-upland border. Transects were 50 m long unless an obvious change in forest characteristics occurred beyond the 50 m point (i.e. a clear-cut) in which case a 100 m transect was surveyed. At points spaced every 5 m (10 m for a 100 m transect) the closest tree in each quarter was measured for basal area and distance to the point on the transect. Stem density of all tree species was calculated using the following equation:

$$\text{Density (trees/hectare)} = \frac{10\,000}{(\text{average distance to point in meters})^2}$$

The proportion hardwood was calculated at the proportion of stems of white birch, trembling aspen, and mountain maple.

1.2.5 Catchment scale assessment

Variables at the catchment scale were calculated using a GIS to analyze information in the Natural Resources and Values Information System (NRVIS) fundamental layers (Ontario Ministry of Natural Resources 2009). Variables included catchment size, proportion of geological landforms, the area of lakes and wetlands within the catchment, the coefficient of variation (CV) of elevation within the catchment, and the area historically harvested within the catchment. Where the geological landform is defined as “bedrock” it is defined as a bedrock form (knob, ridge, or plain) either exposed or overlain by a thin drift veneer, usually of glacial till ground moraine less than 1 m deep, therefore where “bedrock” appears in the text it is not necessarily referring to exposed bedrock (Gartner et al. 1981). The CV elevation was calculated by dividing the standard

deviation by the mean of elevation of each 20X20 m DEM grid cell in the catchment. The proportion of the catchment harvested in the past 10 or 20 years is included to account for variations in age class of the forest, and is not intended as a harvesting “treatment”. Only those sites designated as ‘harvested’ and having adjacent harvesting within the past 6 years are included in the ‘harvested’ treatment. All of these metrics were also calculated for the riparian scale by calculating values within each RCA.

1.2.6 Analysis

Environmental data were divided into the 3 spatial scales (stream habitat, riparian, and catchment scales) and collinear variables were excluded from ordination analyses (variance inflation factor >9, Canoco 4.5). Stream width, riparian width, and chlorophyll *a* were $\log_{10}(x+1)$ transformed to improve normality. Specific analyses will be discussed in the following chapters.

2.0 LANDSCAPE LINKAGES AND HARVESTING EFFECTS ON LOCAL STREAM HABITAT CHARACTERISTICS

2.1 INTRODUCTION

Stream habitats are influenced by factors at several spatial scales in a hierarchical fashion (Frissell et al. 1986). Recognizing the importance of each of these spatial scales is necessary to determine how forest harvesting practices can impact stream habitats at the local scale. The effects of clear-cut forest harvesting on the landscape and on aquatic habitats have been studied extensively. At the whole catchment scale, clear-cut harvesting has been shown to increase water yield (Stednick 1996; Bosch and Hewlett 1982), change soil properties and understory vegetation (Bock and Van Rees, 2002), and alter nutrient dynamics and temperature of streams (Carignan and Steedman 2000). Changes in the aquatic habitat of streams will also influence the biotic community. Aspects of the aquatic ecosystem such as large woody debris, stream flow, temperature, sediments, organic matter inputs, primary production, physical structure, terrestrial microclimate and water quality can be affected by harvesting, and in turn, can impact several aspects of the benthic invertebrate community (see Richardson 2008 for review) Such impacts can be longitudinal, from harvesting in the catchment as a whole, or lateral, from harvesting within the reach contributing area or riparian zone.

Changes in the riparian zone are known to affect changes in several aspects of the stream habitat: photosynthetically active radiation and stream temperature (Kiffney et al. 2003; Sponseller et al. 2001), sediment and organic inputs into the stream (Fisher and Likens 1973), and nutrient processing and filtering from runoff into the stream (Cirimo and McDonnell 1997; Hill 1990; Peterjohn and Correll 1984). Most of these functions were

determined through evaluating the impacts of manipulation of the riparian buffer width or changes in land use.

Forest management strategies tend to be applied at a regional scale, however forest harvesting impacts to aquatic systems may occur across a range of spatial scales.

Kreutzweiser et al. (2008) found that leaf packs in small stream sites adjacent to clear-cuts differed in macroinvertebrate community composition relative to reference sites even with 30-90m forested buffer strips left in place. Such findings raise questions of what landscape elements beyond the standard riparian buffer are linked to local stream habitat and communities. The argument by Buttle (2002) for more hydrologically relevant buffer zones around aquatic habitats includes the need to consider how the habitat is hydrologically linked to the harvested area and the potential for groundwater inputs from local or regional scales. While results may conflict in terms of how effective buffers are in protecting aquatic habitat, a general trend is that greater impacts on water quality occur in sites with larger harvested catchment areas (Buttle 2002). A stream site with a large RCA may have a relatively stronger link to lateral riparian scale characteristics than one with a small RCA. Therefore, due to documented effects of harvesting disturbance including increased inputs of surface runoff and nutrients into aquatic systems, sites with large RCAs have the potential to show a greater response to local harvesting disturbance.

The purpose of this study was to evaluate the linkages between instream habitat and the surrounding terrestrial area and determine how the nature of these linkages may be altered by forest management activities.

My objectives and hypotheses are as follows:

(1) Determine which variables at the riparian and catchment scales were most important in explaining variation in local habitat characteristics. This portion of the study is purely descriptive in nature.

(2) Determine the relative contributions of the riparian and catchment scales in explaining variation in local habitat characteristics and contrast between small and large RCAs. It is hypothesized that stream reaches with large RCAs will have a stronger linkage to the lateral terrestrial area than will reaches with small RCAs. Therefore I predict that the correlation between stream habitat variables and riparian scale variables will be greater at sites with large RCAs than at sites with small RCAs.

(3) Determine the effects of adjacent harvesting on local stream habitat characteristics, and compare the magnitude of effects between small and large RCAs. The influence of riparian and catchment scale variables on the stream habitat in reference and harvested stream sites was also determined. It is hypothesized that uncut buffers will protect stream reaches with small RCAs from harvesting effects, but that large RCAs will be exposed to clear-cut areas and so convey runoff from the harvested area to the stream which may input greater organic matter, nutrients, and runoff heated by solar radiation. Therefore I predict that stream reaches with large RCAs will show significant differences in stream habitat variables compared to reference sites, but that stream reaches with small RCAs will show no difference or smaller differences in stream habitat.

2.2 METHODS

2.2.1 Analysis

Sites were grouped into factors of interest for analysis: All 30 sites, reference sites (n=23), harvested sites (n=7), large RCA sites (n=15), and small RCA sites (n=15). The local scale variables were standardized to z-values and were treated as the “species” matrix in ordination analyses. All ordination analyses were performed in Canoco 4.5 (Biometris, Wageningen, The Netherlands).

To determine patterns in local stream habitat variables a principal components (PCA) ordination was done using the standardized local variables with scaling focused on “inter-species correlations” and species divided by standard deviation and centered. To determine relationships between stream habitat variables and spatial scales, redundancy analysis (RDA) ordinations were done with standardized local habitat variables as the “species”. Comparisons were done with combined riparian and catchment variables, riparian only and catchment only for all 30 sites, and for each site grouping for a total of 15 ordinations.

To determine differences in the local scale variables between reference and harvested sites a multiple response permutation procedure (MRPP) was performed (PCOrd; MjM Software, Glenden Beach, Oregon). A MANOVA was performed (SPSS 16.0.1, SPSS Inc, Chicago, Illinois) to determine which individual variables at the local scale were significantly different between reference and harvested sites and to investigate any interaction effects between harvesting and RCA size class. To facilitate direct

comparisons between variation explained, and correlations of variables in reference and harvested sites, values are reported for the whole reference site grouping (n=23) and for ordinations run with a subset of sites to be equal to the number of harvesting sites (n=7). The subset of sites was determined by randomly selecting 7 sites from the reference group with the same distribution among large and small RCAs as the harvested sites (i.e. n=4 large RCA, and n=3 small RCA). This reduced differences in variance explained for each group resulting from the mathematics of the statistical analysis dependent upon number of sites, and allowed comparison based only on the harvesting condition.

2.3 RESULTS

2.3.1 Habitat characteristics

The stream sites studied covered a wide variety of conditions (see Table 2.1 for summary statistics). Stream width was fairly uniform and averaged 1.4 m wide. Streams were slow flowing with an average velocity of 0.1 m/s. The most variable factors were gradient, substrate and chlorophyll *a*. Stream gradient ranged from 0 to 12 degrees of slope, substrate ranged from 0% fine substrate (high gradient sites dominated by boulder and cobble) to 100% fine substrate (low gradient sites dominated by silt and sand), and chlorophyll *a* ranged from 0.1 to 15.0 mg/m². Stream gradient was omitted from ordination analyses due to high collinearity, as it was significantly negatively correlated with both fine substrate ($R^2 = 0.400$, $p < 0.001$) and riparian width ($R^2 = 0.154$, $p = 0.032$). Other factors were less variable overall but had greater differences between site groupings such as more canopy cover at small RCA sites (85%) than at large RCA sites

Table 2.1. Means (1 SD) of stream habitat and landscape variables given for all sites, and for each of the 4 site sub-groupings

Variable	Abbreviation	RCA size class			Land-use	
		All sites	Large	Small	Reference	Harvested
<i>Local scale habitat</i>						
Stream Gradient (degrees)	Gradient	2.65 (2.97)	1.83 (1.73)	3.47 (3.16)	2.76 (2.81)	2.29 (2.18)
% Canopy Cover	Canopy C	78.17 (21.64)	71.75 (27.79)	84.59 (10.44)	80.64 (18.81)	70.06 (29.42)
Log10 Stream width (m)	Log10strm	1.40 (0.72)	1.31 (0.56)	1.49 (0.87)	1.51 (0.78)	1.04 (0.26)
Stream temp (°C)	Temp	13.33 (3.14)	13.10 (3.43)	13.56 (2.91)	12.34 (2.51)	16.57 (2.93)
Dissolved Oxygen (mg/L)	DO	9.12 (2.20)	8.98 (2.12)	9.27 (2.35)	9.68 (2.17)	7.28 (1.01)
Total woody debris (count)	Total wo	4.00 (1.58)	4.40 (1.40)	3.60 (1.68)	3.87 (1.60)	4.43 (1.51)
Total detritus (abundance scale)	Total de	3.60 (1.90)	4.07 (2.02)	3.13 (1.73)	3.39 (2.04)	4.29 (1.25)
% fine substrate	finesub	43.27 (39.04)	55.47 (40.75)	31.07 (34.31)	40.26 (39.05)	53.14 (40.33)
Water velocity (m/s)	Velocity	0.10 (0.05)	0.10 (0.06)	0.09 (0.04)	0.09 (0.05)	0.11 (0.07)
Total Nitrogen (mg/L)	Total N	0.46 (0.15)	0.52 (0.17)	0.41 (0.12)	0.41 (0.12)	0.65 (0.09)
Log10Chlorophyll a (mg/m ²)	Log10chla	2.17 (3.17)	1.97 (2.57)	2.36 (3.75)	2.13 (3.06)	2.26 (3.76)
<i>Riparian scale landscape</i>						
Size of RCA (sq m) [†]	RCA	1.14E5 (1.47E5)	2.27E (1.32E5)	853 (521)	1.18E5 (1.61E5)	1.00E5 (9.64E4)
Tree density (per ha)	Tree den	4760 (2888)	3935 (3325)	5586 (2184)	5171 (2863)	3413 (2739)
Log10Riparian width (m)	Log10rip	10.75 (13.88)	11.63 (5.79)	9.88 (19.07)	11.19 (15.68)	9.32 (5.15)
Proportion hardwood	Prophard	0.36 (0.26)	0.36 (0.28)	0.36 (0.25)	0.37 (0.27)	0.32 (0.23)
% of RCA cut within 20 years	rca20har	22.72 (45.87)	37.20 (58.60)	8.24 (21.78)	7.23 (1.80)	73.63 (7.09)
% of RCA cut within 10 years	rca10har	18.98 (45.48)	33.65 (59.53)	4.32 (16.73)	2.35 (1.07)	73.63 (7.09)
% of RCA bedrock	rcaBedr	84.99 (33.29)	89.97 (22.97)	80.00 (41.40)	80.42 (3.70)	100 (0)
Coefficient of Variation for elevation in the RCA	rcaCV_elev	0.02 (0.03)	0.04 (0.03)	0.01 (0.01)	0.03 (0.03)	0.01 (0.01)
<i>Catchment scale landscape</i>						
Catchment size (sq m)	Eshed_sqm	9.41E5 (2.55E5)	1.02E6 (3.05E6)	8.62E5 (1.68E5)	9.77E5 (2.72E5)	8.21E5 (1.41E5)
% of catchment bedrock	%Bedrock	94.60 (13.68)	92.92 (15.33)	96.28 (12.10)	92.95 (15.32)	100 (0)
% of catchment cut within 20 years	Harv20	7.84 (13.54)	9.53 (15.01)	6.15 (12.18)	6.51 (12.52)	12.21 (16.79)
% of catchment cut within 10 years	Harv10	2.95 (7.70)	5.12 (10.40)	0.78 (2.11)	3.11 (8.69)	2.44 (2.98)
% of catchment lakes	%Lake	0.88 (1.52)	0.92 (1.47)	0.83 (1.62)	0.62 (1.39)	1.71 (1.74)
% of catchment wetlands	%Wetland	1.12 (2.17)	0.62 (1.28)	1.62 (2.76)	0.83 (2.20)	2.08 (1.92)
Coefficient of Variation for elevation in catchment	CV_elev	0.05 (0.03)	0.05 (0.04)	0.05 (0.03)	0.06 (0.03)	0.02 (0.01)

[†] Scientific notation presented as 1.14 X 10⁵ = 1.14

(72%). More than three quarters of sites had at least 75% canopy cover. Stream temperature ranged from 8.2° C to 21.4° C and was higher at harvested sites than references sites (means of 16.5° C and 12.3° C respectively).

The reach contributing areas of sites were dichotomous by design and ranged from 0.04 to 0.20 hectares in the small size class and from 6.36 to 45.92 hectares in the large size class. Width of the riparian zone was also highly variable ranging from 1 to 78 m wide. Total tree density in the RCA ranged from 971 to 13 330 trees per hectare and tended to be greater in large RCAs and in reference sites. The proportion of hardwood ranged from 0 to 0.90 but the mean was fairly constant among all site groupings. Geology in RCAs was dominated by bedrock; 23 out of all 30 sites had 100% bedrock cover in the RCA. Historical harvesting in the past 10 and 20 years averaged 19% and 23% respectively and was higher in large RCA sites and in recently harvested sites. In 5 of the 8 riparian scale variables variance was significantly greater in large RCA sites than in small RCA sites including RCA size (Levene Statistic (LS) = 42.7, $p < 0.001$), rca20harv (LS = 7.6, $p = 0.01$), rca10harv (LS = 12.2, $p = 0.002$), % bedrock (LS = 4.5, $p = 0.044$), and CV elevation (LS = 34.1, $p < 0.001$).

Catchment size ranged from 45.9 hectares to 146.7 hectares and mean size did not differ between site groupings (MANOVA, RCA: $F_{1,26} = 1.89$, Harvest: $F_{1,26} = 2.49$, $p > 0.1$).

The catchments were dominated by bedrock with 26 of the 30 sites having more than 95% bedrock cover. Catchments had between 0 and 39% harvested in the past 10 years and 0 to 49% harvested in the past 20 years. Lakes covered up to 5% of catchment areas

and wetlands covered up to 10% of catchment areas. Wetlands were significantly negatively correlated with CV elevation in the catchment ($R^2 = 0.16$, $p = 0.03$). The mean topographic relief was constant across all site groupings except for recently harvested sites, in which the CV elevation was significantly lower than reference sites (ANOVA, $F_{1,28} = 8.54$, $p = 0.007$).

2.3.2 Associations between stream habitat and landscape characteristics

Principal components analysis of local scale habitat variables captured 76.1% of the among site variance in 4 axes, and 53.9% in the first 2 axes (33.8% in the first and 20.1% in the second). Two main gradients of variables were identified. The first gradient positioned warmer, nitrogen rich sites at one end and wider, cooler, oxygen rich sites at the other end. The second gradient is nearly orthogonal with the first and positioned faster, more productive (higher chlorophyll *a*) sites at one end and more depositional sites (higher fine sediments, detritus, and woody debris) at the other end. Productivity, as estimated by chlorophyll *a*, tended to be higher at sites with greater velocity, temperature and nitrogen (Fig. 2.1).

Redundancy analysis was used to examine the correlations between local variables and riparian and catchment scale variables (summary Table 2.2). Stream sites that differed in local scale habitat characteristics were separated along 2 gradients of riparian scale variables (Fig. 2.2a). First, sites that were wider and higher in DO were correlated with higher tree density and greater topographic relief, in contrast with sites that had higher nitrogen levels and temperatures which were correlated with reach contributing areas

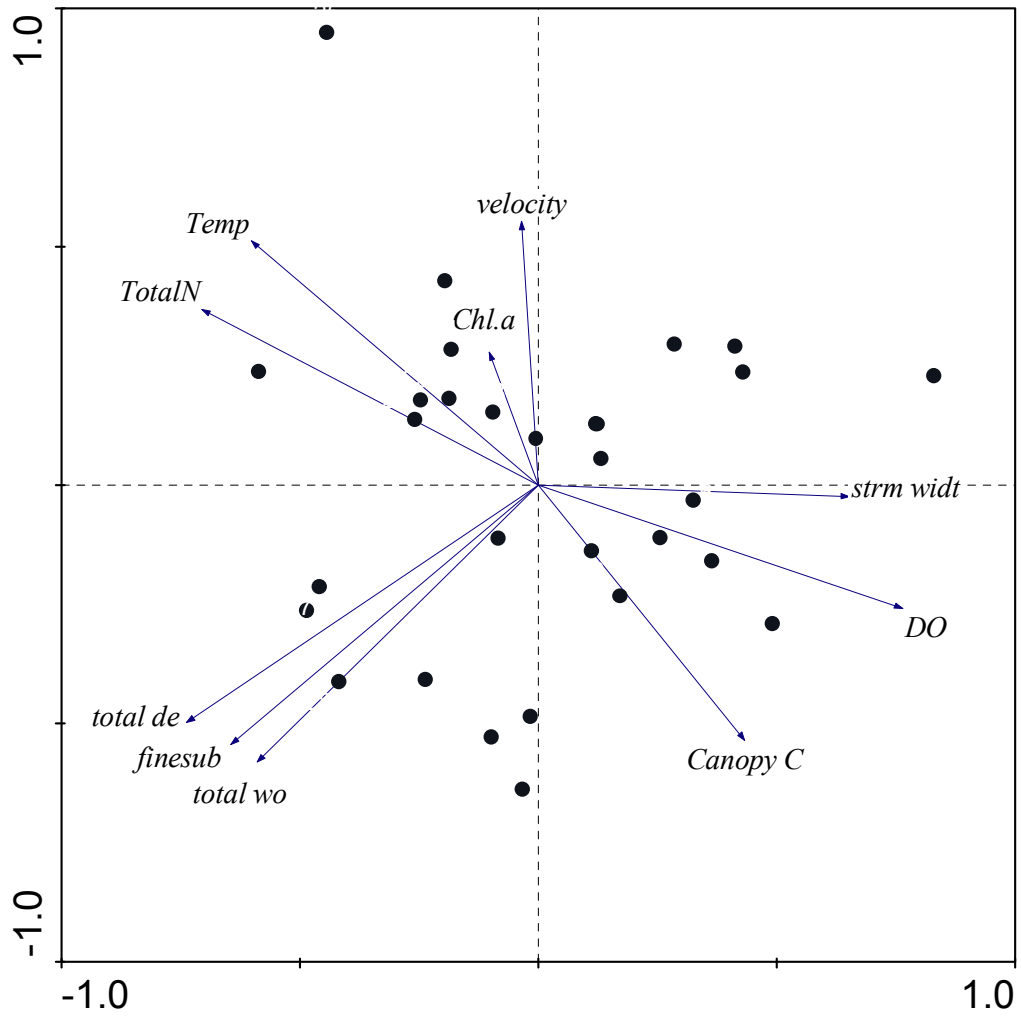


Figure 2.1. Principal components analysis (PCA) ordination (axes 1 and 2) of sites (points) based on standardized local scale habitat variables (vectors). 53.9% of variance in among stream habitat characteristics is captured in these 2 axes.

Table 2.2. Summary of all Redundancy analysis (RDA) ordinations of local stream variables as response variables and riparian and catchment variables as predictor variables

Site grouping	Spatial scale	Variance explained (%)		Strongest variables	Axis correlations		Randomization tests	
		all axes	axes 1&2		1	2	all axes	first axis
All sites	Riparian and Catchment	52.8	32	lg10Rip_	0.5269	0.1491	0.198	0.092
				rcaBedro	0.5007	-0.1475		
				CV_elev_	-0.4994	0.2966		
				rca20har	0.4079	-0.1897		
	Riparian	33	25.7	lg10Rip_	0.5618	0.3309	0.042	0.02
				rcaBedro	0.5142	-0.2624		
				rca20har	0.4305	-0.2392		
				tree Den	-0.3983	0.1521		
	Catchment	24.1	18.1	CV_elev_	0.604	-0.153	0.492	0.224
				.Wetland	-0.3281	-0.1276		
				.Lake	-0.2764	-0.2848		
				.Bedrock	-0.2808	0.1797		
Reference (value adjusted so # sites equal to harvested)†	Riparian and Catchment	61.2 (69.2)	38.2 (61.1)	lg10Rip_	0.6858	0.0142	0.38	0.408
				.Wetland	0.0101	-0.5469		
				CV_elev	-0.0077	0.5428		
				rca	0.1797	0.4735		
	Riparian	39.3 (88.3)	28.9 (70.3)	lg10Rip_	0.7154	-0.159	0.104	0.056
				CV_elev	-0.041	-0.5201		
				prophard	-0.4342	-0.2906		
				rcaBedr	0.3813	0.2901		
	Catchment	24.5 (68.0)	16.3 (58.5)	CV_elev_	0.6492	0.0655	0.874	0.806
				.Wetland	-0.5222	0.1535		
				Eshd_sqm	-0.3693	-0.0912		
				.Lake	-0.2976	0.1243		
Harvested	Riparian and Catchment	89.5	71.3	prophard	0.9161	-0.1726	0.268	0.448
				.Wetland	-0.6707	-0.1516		
				Eshd_sqm	-0.6228	-0.4766		
				rca20har	0.6185	0.4669		
	Riparian	85.6	71.6	prophard	0.9143	-0.2236	0.446	0.338
				rca20har	0.6139	0.4656		
				tree Den	-0.4559	-0.0728		
				rcaCV_el	0.3654	-0.3285		
	Catchment	70.6	54.8	.Lake	-0.7753	0.06	0.39	0.554
				Eshd_sqm	-0.7368	0.1273		
				.Wetland	-0.7057	-0.4172		
				CV_elev	-0.294	0.6115		

† For ease of comparison and graphical interpretation (in Fig. 2.3), reference group was adjusted to include an equal number of sites to harvested group (n=7). This was done by randomly selecting 7 reference sites from the same distribution between large and small RCAs (n=4 large RCA, and n=3 small RCA) and re-running RDA ordinations using the randomly selected 7 sites. Adjusted values are reported in parentheses below the unadjusted values for the whole reference group (n=23).

Table 2.2 con't

Site grouping	Spatial scale	Variance explained (%)		Strongest variables	Axis correlations		Randomization tests	
		all axes	axes 1&2		1	2	all axes	first axis
Small RCA	Riparian and Catchment	77.1	76.7	.Harv20	0.5036	-0.0282	0.254	0.21
				Eshd_sqm	-0.4495	-0.0195		
				tree Den	0.3246	-0.0654		
				CV_elev_	0.048	0.3206		
	Riparian	76.3	76	rca20har	0.61	-0.2203	0.264	0.222
				tree Den	0.3231	-0.1554		
				rca	0.292	0.299		
				lg10Rip_	0.2636	-0.2009		
	Catchment	67.9	67.6	.Harv20	0.5027	0.075	0.146	0.154
				Eshd_sqm	-0.4493	-0.0278		
				CV_elev_	0.051	-0.2989		
				.Wetland	-0.2527	-0.1981		
Large RCA	Riparian and Catchment	82.3	82.2	.Wetland	0.4325	0.5466	0.194	0.296
				.Harv20	-0.5324	0.0156		
				CV_elev_	-0.2332	-0.5463		
				prophard	-0.4876	-0.4035		
	Riparian	85	84.9	tree Den	-0.3559	-0.4823	0.128	0.314
				prophard	-0.4699	-0.4573		
				rca20har	0.1005	-0.3912		
				rcaCV_el	-0.1345	-0.5805		
	Catchment	47.4	47.3	.Wetland	0.568	0.2133	0.544	0.526
				.Harv20	-0.5356	0.2792		
				Eshd_sqm	0.0984	0.3727		
				CV_elev_	-0.3658	-0.3125		

with a higher proportion of bedrock and historical harvesting. Along the second gradient, depositional sites with higher fine substrate, detritus and woody debris were correlated with wider riparian zones, whereas sites with higher levels of DO were correlated with a higher proportion of hardwood in the RCA.

Catchment scale variables showed a similar pattern with sites differing in local habitat characteristics separated along 2 main gradients (Fig. 2.2b). The sites with greater DO and canopy cover were correlated with greater topographic relief in the catchment, contrasting with faster more productive sites being correlated with a greater proportion of bedrock in the catchment. The second gradient has warmer, nitrogen rich, depositional streams correlated with a greater proportion of lakes and wetlands in the catchment.

2.3.3 Relative contribution of spatial scales

For all groupings of sites (all sites, reference, harvested, large RCA, and small RCA), riparian scale variables contributed more to explaining variation in local scale habitat characteristics than did catchment scale variables (Fig. 2.3). Riparian scale variables explained between 33% (all sites) and 88.3% (reference sites) of variation in local habitat characteristics and the catchment scale explained between 24.1% (all sites) and 70.6% (harvested sites) of variation in local habitat characteristics (from RDA analyses, Table 2.2). The greatest difference in the contribution of each spatial scale to explaining local scale variation was in the large RCA sites, where riparian scale variables explained almost 40% more variation than catchment scale variables.

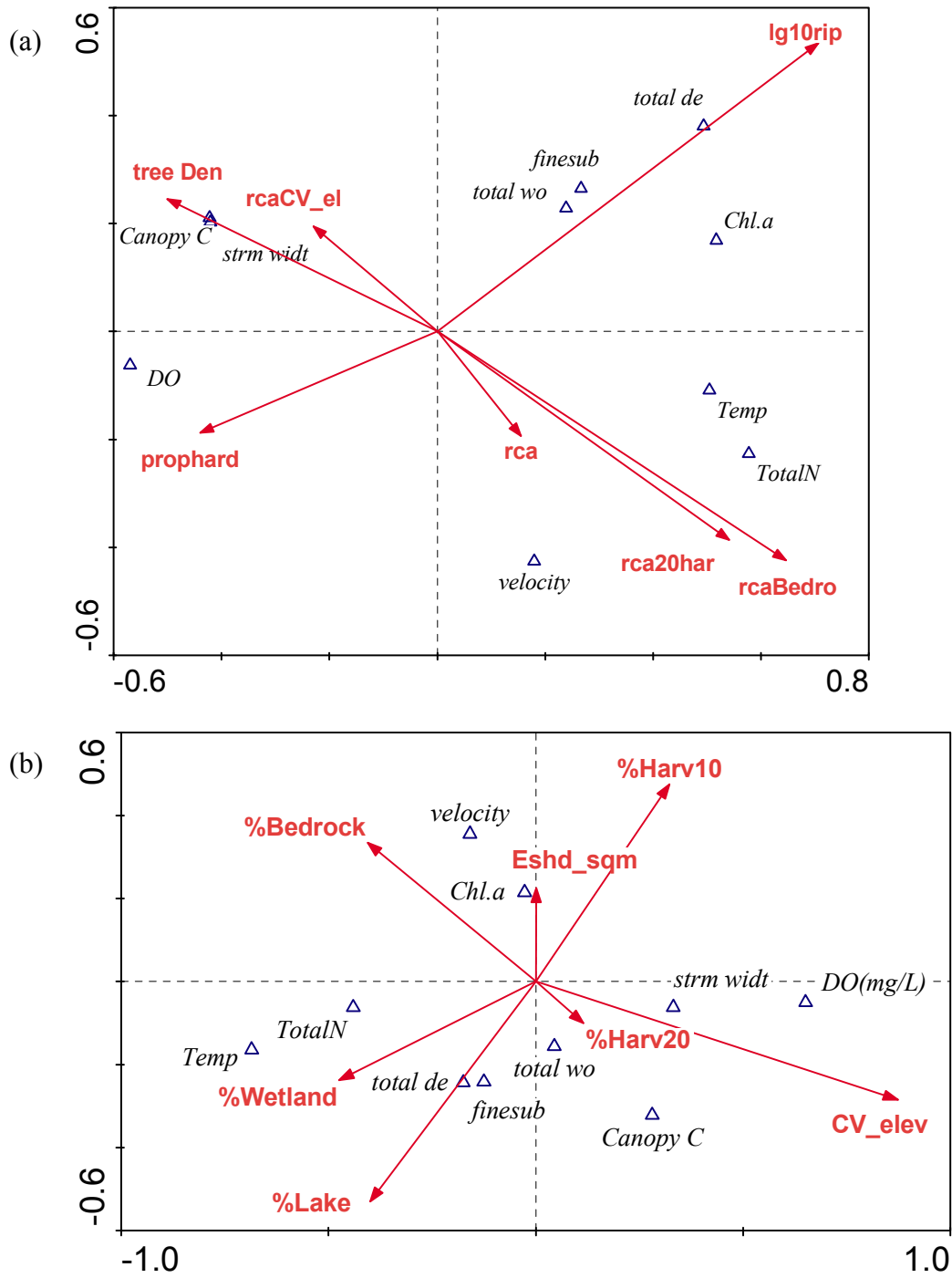


Figure 2.2. Redundancy analysis (RDA) Ordinations (axes 1 and 2) of local scale environmental variables as the response matrix (points) and (a) riparian scale variables and (b) catchment scale variables (vectors) as the predictor matrices

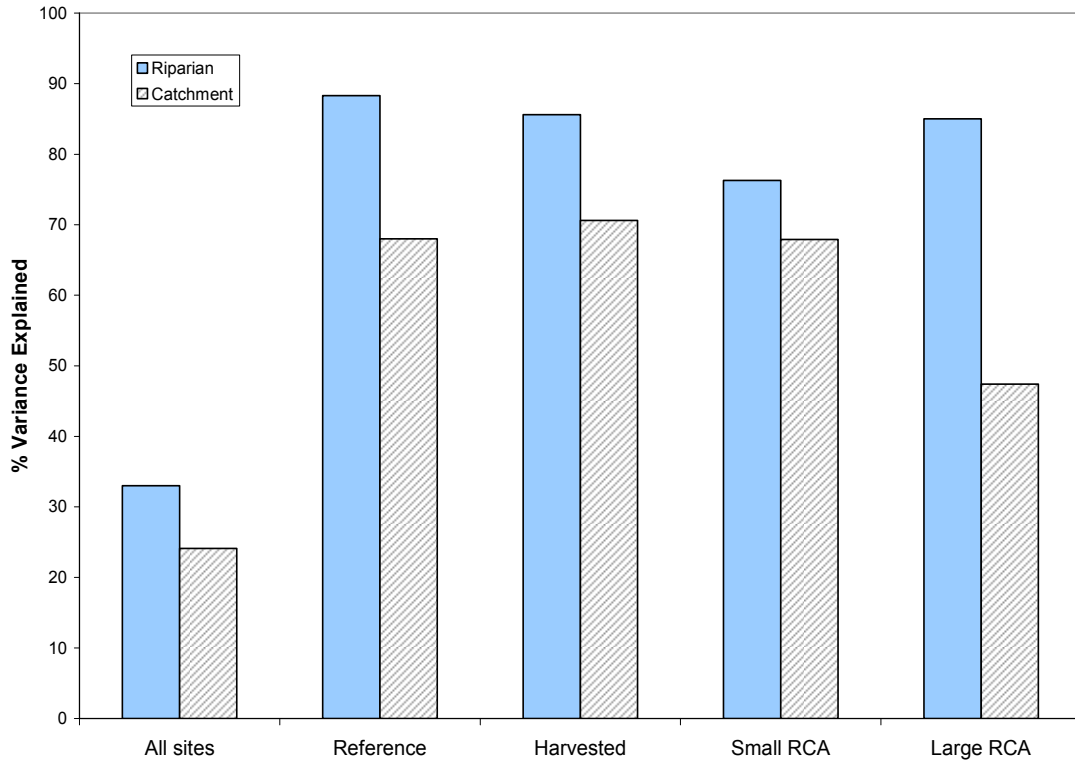


Figure 2.3. Amount of variance in local scale environmental variables explained by riparian and catchment scale variables in all sites, and each site grouping category. “Reference” category adjusted to include number of sites equal to “Harvested” category. From RDA analyses, Table 2.

2.3.4 Effects of harvesting

Characteristics of local habitats differed significantly between reference and harvested sites (MRPP, $A=0.05$, $p=0.001$). Differences in individual local habitat variables between RCA classes and harvesting treatments were evaluated using MANOVA. Stream temperature was on average 4°C warmer in harvested sites ($F_{1,26} = 13.50$; $p = 0.001$, Fig. 2.4a) and total nitrogen was more than 50% higher at harvested sites ($F_{1,26} = 23.84$; $p < 0.001$, Fig. 2.4c). Dissolved oxygen was on average 2.5mg/L lower at harvested sites ($F_{1,26} = 7.98$; $p = 0.009$, Fig. 2.4b). The only significant interaction effect between RCA and harvesting was total woody debris ($F_{1,26} = 5.97$, $p = 0.022$) which did not differ between reference and harvested sites in large RCA sites but in small RCA sites was nearly double in harvested sites than in reference sites (Fig. 2.4d).

In both reference and harvested sites, riparian scale variables contributed more explanatory power for variation in local scale characteristics (88.3% and 85.6% respectively) than catchment scale variables (68.0% and 70.6%, respectively) based on RDA analysis (Table 2.2). The same catchment scale variables had the strongest correlations with local scale variation in both reference and harvested sites (Table 2.2). The riparian scale variables most strongly correlated with variation in local habitat differed between reference and harvested sites. In reference sites the variables with the strongest correlations were mostly topographical (bedrock, CV elevation, and riparian width) but also included the proportion hardwood (Fig. 2.5a), whereas in harvested sites the variables with the strongest correlations were related to forest cover (proportion hardwood, harvesting in the past 20 years, and total tree density) (Fig. 2.5b).

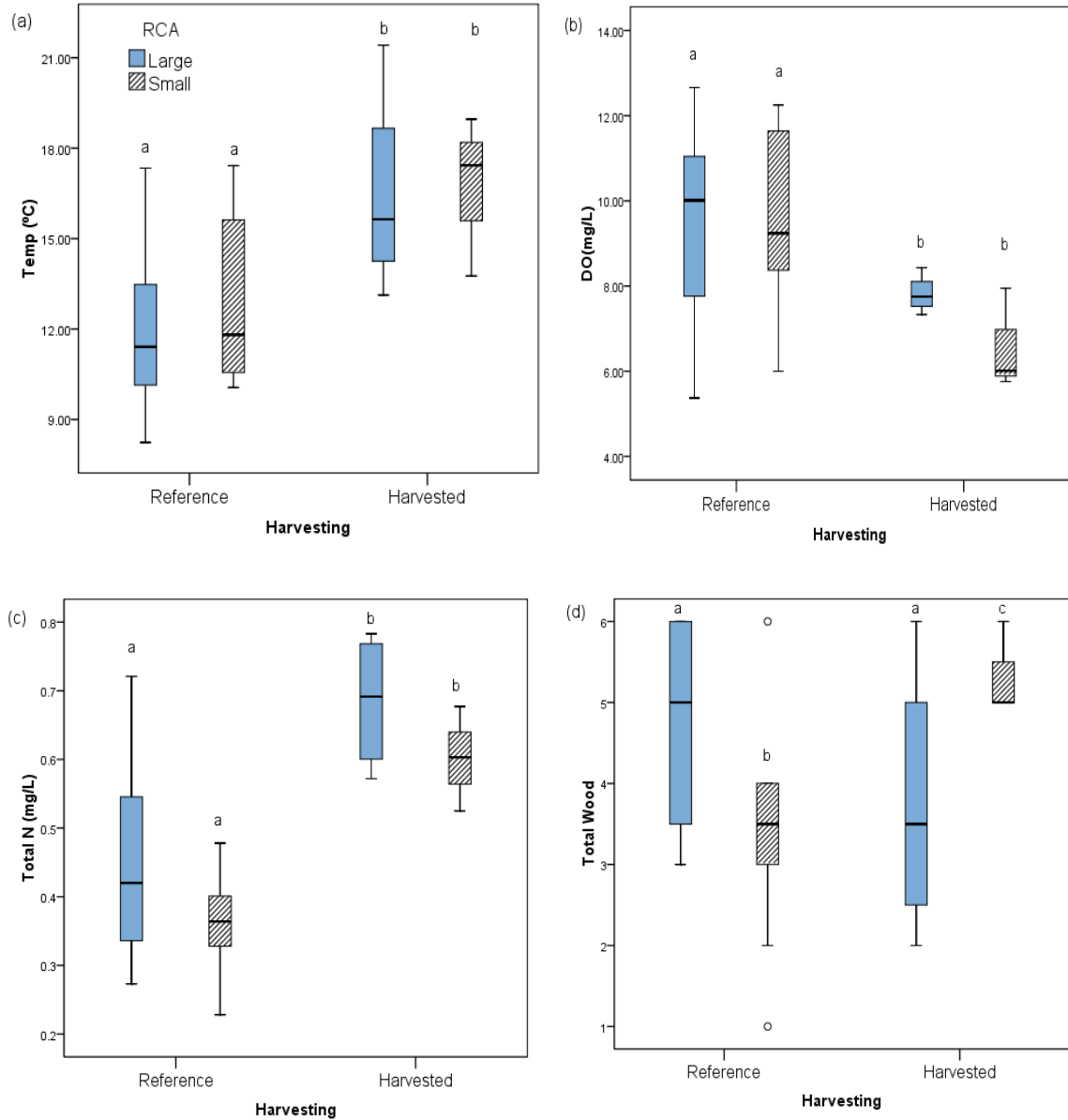


Figure 2.4. Boxplots of local scale habitat variables that varied significantly between reference and harvested sites: (a) Stream temperature, (b) Dissolved Oxygen, (c) Total nitrogen, and (d) Woody debris. Solid boxes show large RCA sites, striped boxes show small RCA sites. Solid line indicates the median, boxes indicate inter-quartile range, and whiskers indicate the range. Open circles represent outliers more than 3 SD from median. Different letters denote significant differences between means determined by a MANOVA using RCA size and harvesting as factors ($p < 0.05$). For woody debris (d) post-hoc one way ANOVAs were done to separate the interaction effect between RCA size and harvesting.

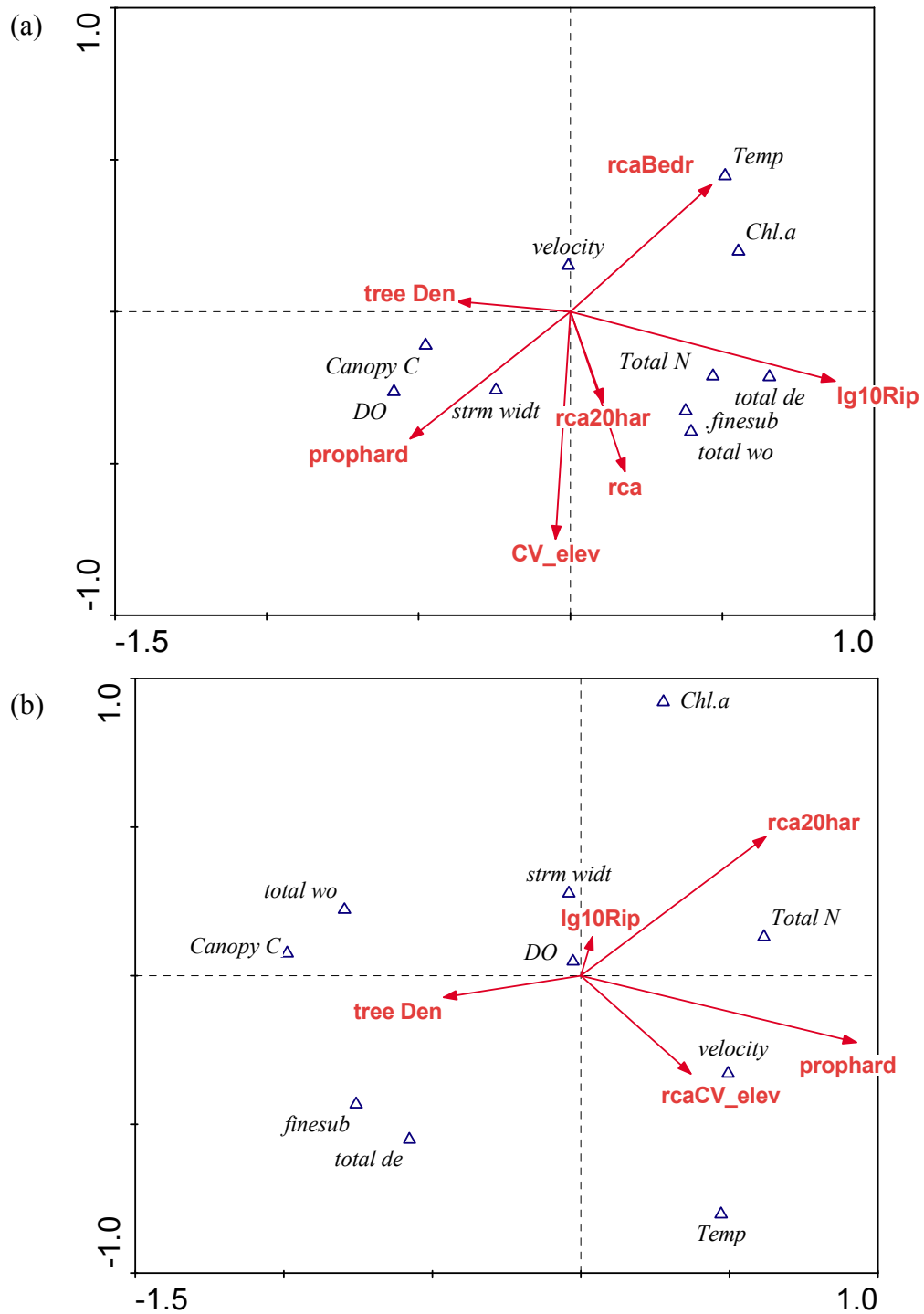


Figure 2.5. Redundancy analysis (RDA) ordinations (axes 1 and 2) of local environmental variables as the response matrix (points) and riparian scale variables as the predictor matrix (vectors) for (a) reference sites, and (b) harvested sites. Forward selection was used to maintain n-2 explanatory (riparian scale) variables resulting in fewer variables retained in the ordination of harvested sites.

2.4 DISCUSSION

2.4.1 Associations between stream habitat and landscape characteristics

Headwater streams tend to be grouped together as a functional type when studying variation in stream conditions (e.g. Vannote et al. 1980). However, these results illustrate the large amount of variation within headwater streams on the boreal shield. Variation in local habitat characteristics is associated with linkages to the surrounding terrestrial environment within the reach contributing area and within the entire catchment. The strength of linkages between the aquatic and terrestrial environments and the variables driving those associations were found to vary with topography and land use in the RCA.

The link between aquatic systems and the surrounding terrestrial environment is well accepted (Vannote et al. 1980), but only recently has there been more emphasis on the spatial scale at which those linkages occur. Many of the recent studies on spatial scale are interested in how anthropogenic land use at these scales is important (e.g. Sponseller et al. 2001), but I have identified the naturally varying factors at each scale which are most closely associated with instream habitat. At the riparian scale, riparian zone width, bedrock, and forest density were most strongly correlated with variation in local habitat. Sites with greater riparian widths tended to have more detritus, fine substrate, and chlorophyll *a*. The proportion of fine sediment and detritus particles will be higher in low velocity stream segments (Allan 1995) which tend to occur in segments with a shallower gradient. The correlations between gradient and both riparian width and fine substrate indicates that the relationship between riparian width and fine substrate is correlational rather than causal and is mediated by topography.

Stream sites could be classified along a gradient of local habitat characteristics from wide, cool, oxygen-rich streams to warmer, depositional, nitrogen-rich streams.

Chlorophyll *a* concentration was not associated with one end of the gradient, but was greater in warm, nitrogen-rich sites, with larger substrate and higher velocity.

Chlorophyll *a* and periphyton biomass have been shown to increase with velocity, especially under high light-levels (McIntire 1968). The correlation with velocity may also be related to the size of substrate particles. Different algal species will be abundant on rocks and large substrate as opposed to fine, silty substrates (Hynes 1970), and sites with greater velocity in this study tended to have larger rocky substrate. Nitrogen has also shown, in some cases, to be limiting to periphyton growth, especially in nutrient-poor systems (Allan 1995) such as the boreal shield streams in NW Ontario.

The relationship of chlorophyll *a* with riparian zone width may be a function of the degree of shading or nutrient input from the banks. Riparian width was negatively correlated with canopy cover. Sites with wider riparian zones tended to be dominated by shrubs, with less canopy cover by mature trees which may allow more light to penetrate to the stream and increase algae growth. Primary production in nutrient-poor systems may also be limited by nitrogen or phosphorus levels (Allan 1995). Nitrogen retention tends to increase with water residence time in the riparian zone and soil moisture saturation (Cirimo and McDonnell 1997), so nitrogen in surface and subsurface runoff can be depleted by up to 90% in riparian zones before reaching the stream (Hill 1996). Therefore lower nitrogen levels would be expected at sites with wider saturated riparian

zones. Alder leaf litter, however, tends to have more available nitrogen than other deciduous species (Goldman 1961) and sites in this study with a wide riparian zone did tend to be dominated by the shrub *Alnus rugosa* (speckled alder) (pers. obs.). The high density of speckled alder may be obscuring the effect of increased nitrogen retention.

Stream sites with higher temperature and total nitrogen tended to be correlated with RCAs characterized by a high proportion of bedrock. Soil nitrogen availability has been shown to increase with scarification and herbicide treatments on boreal sites after harvesting (Munson and Timmer 1995), both of which are common silvicultural practices in the Nipigon forest (Leale, C. Nipigon Area Forester, pers. comm.). Increased nitrogen levels at sites with high levels of historical harvesting may be a long term effect of runoff from these harvested areas into the stream. Stream temperature has been shown to be influenced by local topography (Caissie 2006) and stream reaches with large inputs of groundwater can be as much as 10°C cooler than the surrounding stream reaches (Smith and Lavis 1975). Reaches in this study with a high proportion of bedrock in the RCA would limit the amount of possible subsurface flow, with runoff being exposed to solar radiation and potentially increasing the temperature of the stream. The warmer temperatures and greater nitrogen concentration may also be the results of water retention in the catchment, as discussed below.

Catchment scale variables most strongly correlated with variation in local habitat characteristics were topographic relief, percent wetlands and lakes in the catchment, and percent bedrock in the catchment. Bedrock in the catchment was negatively correlated

with topographic relief and was most closely correlated with stream velocity, and to some extent, temperature and nitrogen. Discharge was omitted from my ordination analyses due to collinearity with velocity, but storage of water in soils generally reduces runoff and stream discharge (Chang 2003). Landscapes with lower topographic relief and shallower soil depth will have more surface flow (Hinton et al. 1993) which could increase water input to the stream in sites associated with more exposed bedrock in the catchment resulting in higher water velocity and discharge.

Ordination analyses showed a gradient between sites with high topographic relief and high DO, and sites with high amounts of bedrock cover and higher stream temperature. Greater topographic relief and less exposed bedrock (conversely, greater soil depth and forest cover) could result in greater subsurface flow which, when discharged into the stream, can lower the stream temperature and increase DO (Chang 2003). In this study catchment topography was also negatively related with total nitrogen which has been shown to be an important influence in many other aspects of water chemistry in lakes such as chlorophyll *a*, phosphorus, and dissolved organic carbon (D'Arcy and Carignan 1997).

Catchments with higher proportions of wetlands or lakes were strongly correlated with sites with higher temperature, total nitrogen, detritus and proportion of fine substrate. Wetlands are well documented to remove nutrients from runoff and act as a sink for nitrogen and phosphorus (Whigham et al. 1988), however different conditions can change the interaction between wetlands and water fluxes. Saturation of the wetland with

phosphorus (Richardson 1985), extremely dry seasons allowing re-oxidation (Devito and Hill 1997), or flooding (Hemond and Benoit 1988) can flush out nutrients creating a net export from the wetland. The spring preceding this study had extreme amounts of rain (194mm in June vs. the average 85mm in Thunder Bay) causing flooding, which may have flushed stored nutrients and sediments from wetlands, and increased nitrogen levels and fine sediments in stream sites with a larger proportion of wetlands in the catchment. Greater water retention in the catchment in the form of lakes and wetlands may allow for greater warming of surface water which, when flushed into the stream, can potentially increase the temperature of the stream.

2.4.2 Relative contribution of spatial scales

I found that in every grouping of sites, riparian scale variables explained more variation in local stream habitat characteristics than catchment scale variables. Most studies involving distinct spatial scales are monitoring the influence on a biotic community (algae, macroinvertebrates, or fish) rather than physical habitat. These results are consistent with several studies that have found intermediate-scale variables covering the lateral riparian area 5-100m wide along a stream reach of 200-500m to have the strongest influence on in-stream communities (Sponseller et al. 2001; Feld and Hering 2007; Weigel et al. 2003). Sponseller et al. (2001) focused on the effect of disturbance at each scale and found that disturbance at the intermediate scale has a larger effect on stream biotic communities than disturbance at a larger catchment scale. Weigel et al. (2003) found that the relative contributions of spatial scale were dependent on the community attributes being studied; riparian and catchment were approximately equal in explaining

variation in metrics including invertebrate feeding guild composition, but riparian scale variables explained more variation in relative abundance of taxa. By contrast, in a study to develop a habitat model for Atlantic salmon, Bouchard and Boisclair (2008) found that only local and longitudinal factors contributed to the model. Lateral factors were not significant in predicting salmon habitat.

The greatest difference in explanatory power of the riparian and catchment scales in this study was in sites with a large RCA, where riparian scale variables explained almost 40% more variation than catchment scale variables. I hypothesize that this is the result of the riparian scale factors being inherently more variable themselves in large RCAs. A greater possible range of characteristics in the RCA may have greater explanatory power for a greater range of local habitat characteristics.

2.4.3 Effects of harvesting

Studies documenting the effect of harvesting on aquatic habitat have often found differences when harvesting right to the stream edge (Newbold et al. 1980), but that standard forested buffer strips are effective in protecting the stream characteristics (Kreutzweiser et al. 2008). I found significant differences in stream habitat characteristics in harvested areas despite streams being protected by a standard 30-50m forested buffer. The local habitat characteristics that differed significantly between reference and harvested sites were stream temperature, total nitrogen, dissolved oxygen, and woody debris. Increases in stream temperature after harvesting have been well documented and are mostly due to increased solar radiation after canopy removal

(Kiffney et al. 2003). When studying the influence of multiple spatial scales, Sponseller et al. (2001) found that 93% of variation in stream temperature could be explained by forest cover at the riparian scale. My results agree with this increase in stream temperature, however I found no difference in canopy cover between reference and harvested streams which would allow for increased solar radiation. In this case, increased temperatures in harvested stream sites may be a result of surface runoff in clear-cut areas being exposed to more radiation, and groundwater being warmed through increased soil temperature, which may then contribute to increased stream temperature when those lateral inputs reach the stream (Johnson and Jones 2000). There are also some studies that have found no effect of harvesting with a riparian buffer (Wilkerson et al. 2006), or even decreased stream temperatures after harvesting (for example Jackson et al. 2001) possibly due to increased blowdown over the stream causing shading.

My results, showing significantly higher nitrogen levels in harvested sites, agree with many studies showing increased nutrient flux to boreal lakes (e.g. Carignan et al. 2000) and small streams (e.g. Wang et al. 2006) after clear-cut harvesting and post-harvesting practices such as scarification and herbicide treatments (Munson and Timmer 1995). These increases could be due to reduced uptake by plants (Munson and Timmer 1995) and increased runoff from harvested areas (Steedman 2000). The prolonged increases (up to 6 years post-harvest in this case) of total N in harvested streams may be a result of increased decomposition occurring in clear-cut areas. Hazlett et al. (2007) found that incubated soil samples from 12 year-old clear-cuts released 75 times more Nitrate-nitrogen than paired reference sites, demonstrating the potential for increased export of

nitrogen from harvested sites many years post-harvest. As the harvested areas in this study were treated with herbicide, they remained relatively free of ground cover for an extended time after harvesting. A study by Kreutzweiser et al. (2008) in low-order boreal shield streams, however, found no significant difference in nitrogen levels in harvested sites. This discrepancy may be explained in some part, by the larger streams being studied by Kreutzweiser, which would be expected to have weaker linkages to terrestrial area (McGlynn and Seibert 2003; Vannote et al. 1980) and therefore smaller impacts from disturbance to the surrounding land. An alternative explanation for the increased levels of total N in the recently harvested sites in this study is the correlation with landscape variables indicating low topographic relief, and greater % wetlands (see table 2.1). Dissolved organic material export tends to increase with lower topographic relief (DOC in D'Arcy and Carignan 1997) and with increased wetlands (TON in Devito et al. 1989) which would also explain higher levels of total N in streams with these characteristics. As it is more likely for catchments with lower topographic relief to be selected for harvesting, this relationship would be correlational rather than causal.

The significant interaction of harvesting and RCA size on woody debris was likely influenced by one anomalous site. One harvested, small RCA site had considerably more windthrow from the forested buffer presumably from the buffer edge being on a ridge exposed to the clear-cut, resulting in significantly higher amounts of woody debris in the stream site.

The relative contributions of riparian and catchment scale variables remained approximately equal for both reference and harvested sites with riparian scale variables explaining more variation (88.3% in reference and 85.6% in harvested) in stream habitat characteristics than catchment scale variables (68.0% and 70.6% respectively) for both groups of sites. The difference in the stream-to-landscape relationship was in the variables at the riparian scale most correlated with in-stream variability. Physical and chemical stream characteristics such as temperature, substrate, and nitrogen have been shown to vary with riparian scale forest cover (Sponseller et al. 2001). The stronger correlation between stream habitat and forest-related variables (such as tree density and proportion hardwood) at harvested sites may be due to greater variation in forest-related variables and less variation in topographic variables (such as CV elevation). In the Nipigon Forest Management Plan rugged sites dominated by steep to rough slopes, and bedrock are deemed extremely difficult to harvest (Ontario Ministry of Natural Resources 2008), so sites with a lower CV elevation and less variation in bedrock forms will naturally be selected for harvesting. Therefore the strong correlation with forest cover variables at harvested sites (and the relatively weak correlation with topographic variables) may be coincident with suitability of the site for harvesting, rather than a result of harvesting.

When considering the interaction of harvesting and RCA factors on stream habitat conditions, the sample size becomes too small to draw conclusions regarding differences in response to harvesting between RCA sizes. While it is demonstrated that stream reaches with a large RCA have a stronger linkage to the lateral terrestrial area, there is no

evidence for stronger impacts due to harvesting at sites with large RCAs compared to sites with small RCAs. There is either no difference in the magnitude of impacts (differences in temperature, DO, and nitrogen) between RCA size classes, or the difference is actually slightly greater in stream reaches with a small RCA. This may be the result of greater buffering capacity of riparian zones at stream sites with large RCAs. Large RCA sites tended to be correlated with wider riparian zones which may then be able to mitigate inputs of excess nutrients and warmer surface runoff through retention by riparian plants, and input of cooler groundwater into the stream.

My first hypothesis, that stream reaches with large RCAs have tighter linkages with the lateral terrestrial area than stream reaches with small RCAs, is supported. This can generate new hypotheses based around mechanisms for this linkage such as testing the prediction that surface and subsurface runoff inputs into large RCA stream reaches is greater than at small RCA reaches. My second hypothesis, however, that buffers will protect stream reaches with small RCAs and that reaches with large RCAs will show greater impacts of harvesting disturbance is not supported. If the differences in stream habitat are caused by the adjacent clear-cut at harvested sites, it is clear that the forested buffer is not protecting the stream from disturbance impacts. This can generate new hypotheses based on mechanisms for harvesting impacts to reach streams through protective buffers, such as testing the prediction that surface runoff and groundwater is warmed through greater exposure to solar radiation in clear-cuts and therefore increases the temperature of the stream into which it flows. It is clear, however, from these results that stream habitats are influenced by terrestrial variables at several spatial scales. The

correlation between stream habitat and terrestrial variables at different spatial scales is influenced by the local topography and in turn, can mediate the effects of harvesting disturbance on stream characteristics.

3.0 LATERAL AND LONGITUDINAL SOURCES OF VARIABILITY IN BENTHIC MACROINVERTEBRATE COMMUNITY STRUCTURE

3.1 INTRODUCTION

Aquatic invertebrate community structure can be influenced by many factors at several spatial scales. The most immediate influence is the local aquatic habitat, which can in turn be affected by lateral factors at the riparian scale and longitudinal factors at the catchment scale. In small catchments, local stream habitat characteristics are the dominant factors in structuring invertebrate communities (Brosse et al. 2003; Corkum 1992). Some studies however, have shown greater importance of variables at the intermediate (riparian) scale (Sponseller et al. 2001; Feld and Hering 2007). Large scale (catchment) variables have been shown to be the most important factor distinguishing between invertebrate communities over large regional areas (Corkum 1989), supporting the idea of hierarchical landscape controls on aquatic systems (Frissell et al. 1986).

A great deal of research effort has been dedicated to determining how local habitat characteristics affect invertebrate community assemblages. Corkum (1989) found that at the local scale flow velocity and depth were the primary factors determining site groupings, while Rabeni and Minshall (1977) found the substratum-detritus interaction to be the dominant influence followed by current velocity and siltation. The feeding strategies of invertebrates can have a large impact on how they respond to environmental factors as described by Cummins and Klug (1979), and demonstrated by Peeters et al. (2004) in their study showing that food resource quality will affect invertebrate distribution. Food quality can be related to nutrient concentrations in the stream, which have also been shown to have an effect on invertebrate abundance and community

composition (Hershey et al. 1988; Wang et al. 2007; Perrin and Richardson 1997), however these results were found in relation to unnaturally high levels of nitrogen and phosphorus either through agricultural inputs or experimental addition.

Riparian scale and catchment scale factors can influence the local habitat several ways as seen in section 2, and therefore can also affect the structure of macroinvertebrate communities. For example, the structure of the riparian forest affects the input of leaf litter to the stream which is an important food resource for benthic invertebrates (Cummins 1974; Vannote et al. 1980; Hernandez et al. 2005). The type of riparian forest influences the type of allochthonous inputs to the stream: young deciduous forests tend to contribute more labile and particulate organic material, whereas young coniferous forests contribute less particulate organics but more large woody debris to act as microhabitat for invertebrates (Hernandez et al. 2005). Inputs of nutrients from riparian vegetation and soils can also affect food resources through growth of periphyton (Wang et al. 2007) and microbial communities (Hershey et al. 1988). Shading and the timing of leaf emergence can also affect primary productivity, creating temporal variation in autochthonous energy sources and the associated invertebrate consumers (Hill et al. 2001). Light penetration, and groundwater inputs can both affect the stream temperature, which in turn can influence several aspects of the invertebrate community including growth, development, species interactions, and consumer-resource dynamics (Richardson 2008). Catchment scale factors can also affect invertebrate communities with variation in geomorphology creating heterogeneous stream habitat (Brosse et al. 2003) and influencing flow regimes which can limit invertebrate taxa with varying life histories (Konrad et al. 2008). For

example, the dominant geomorphological forms in a catchment can influence the type of substrate present in the stream habitat which will influence the invertebrate community based on preferences for large substrate particles (erosional taxa) or fine sediments (burrowers) (Richards et al. 1997).

The linkages between local stream habitat and riparian and catchment scale factors will affect how strongly invertebrate community structure is associated with factors at each spatial scale. Due to the topographic controls in delineating the reach contributing area (RCA), stream sites with large RCAs have the potential for stronger linkages to the lateral landscape factors (see section 2). Macroinvertebrate communities would then be expected to differ between stream sites with large RCAs and small RCAs, and have different correlations with riparian and catchment scale variables.

Forest harvesting impacts on small streams and the macroinvertebrate community can also be mediated by topographic controls and the linkage between the stream and the harvested area. Several studies have demonstrated that benthic macroinvertebrate communities can be impacted by forest harvesting in the stream catchment (Carignan and Steedman 2000, Hernandez et al. 2005, Challen 2002). Such impacts can occur through increased light, discharge, sediment runoff, alteration of basal resources, and temperature effects after harvesting (Richardson 2008). Differences in buffer width have also been shown to affect invertebrate communities in terms of colonization (Negishi and Richardson 2006), abundance (Kiffney et al. 2003; Stone and Wallace 1998; Nislow and

Lowe 2006), diversity indices (Newbold et al. 1980), and community composition (Moldenke and Ver Linden 2007; Nislow and Lowe 2006; Stone and Wallace 1998). In stream reaches with a large RCA, the linkages between streams and their adjacent terrestrial environment are hypothesized to be greater than in reaches with a small RCA, thereby potentially increasing the impact of all the above disturbances following harvesting. The magnitude of harvesting impacts on invertebrate communities is then expected to be greater in reaches with large RCAs than in those with small RCAs.

The purpose of this section of my study was to evaluate the linkages between benthic macroinvertebrate communities and the surrounding terrestrial environment and determine how the nature of these linkages may be altered by local topography, and how they may affect harvesting impacts. My objectives and hypotheses are as follows:

(1) Determine which variables at the local, riparian, and catchment scales are most strongly associated with variation in the structure of the benthic invertebrate community. This section is purely descriptive in nature.

(2) Determine if the composition of benthic invertebrate taxa or feeding guilds differs between stream reaches with small and large RCAs. It is hypothesized that the difference in invertebrate community will be most evident in functional feeding guild structure based on the differences in stream habitat found between large and small RCAs.

Therefore I predict that the overall taxonomic composition of the invertebrate

community, and the proportions of functional feeding guilds will differ between RCA size classes.

(3) Determine differences in the relative contribution of spatial scales, and variables at each spatial scale to explain variation in the benthic macroinvertebrate community between stream reaches with small and large RCAs. I hypothesize that stream reaches with large RCAs will have stronger linkages to the lateral terrestrial area than stream reaches with small RCAs. Therefore I predict that invertebrate community taxonomic and feeding guild structure will have stronger correlations with riparian scale variables at sites with large RCAs than at sites with small RCAs.

(4) Determine if the invertebrate community assemblages differ between reference and harvested sites. I hypothesize that based on demonstrated harvesting impacts on stream habitat, and historical evidence in the literature, the invertebrate community will differ between reference and harvested sites. Therefore I predict that the overall community structure will differ at harvested sites and that relative abundances of taxa tolerant to disturbance will be greater at harvested sites.

(5) Determine if the magnitude of those harvesting impacts differed between RCA size classes. I hypothesize that forested buffers will protect the invertebrate community in stream reaches with small RCAs but that stream sites with large RCAs are still hydrologically linked to the harvested area, which would transmit harvesting impacts to

the stream. Therefore I predict differences in invertebrate community composition and metrics to be greater at harvested sites with large RCAs.

3.2 METHODS

3.2.1 Invertebrate assessment

Three replicate invertebrate collections were done at each sampling reach. Samples were collected with a modified Surber sampler; a 30x30cm area of the stream bed was scrubbed and debris and invertebrates were swept into a D-net with 500 μ m mesh held just downstream of the net. Invertebrates were preserved in 75% ethanol and were sorted and identified under a microscope. Invertebrates were identified to genus where possible with Chironomidae and Simuliidae remaining at the family level and non-insect taxa identified to order. Invertebrate taxa were assigned to functional feeding guilds according to Merritt and Cummins (1996) based on generic level classification. Due to the lack of taxonomic resolution and wide range of feeding strategies, Chironomidae was excluded from the feeding guild analysis. Metrics summarizing the invertebrate community were calculated including: total abundance, total richness, evenness, % Chironomidae, % EPT and EPT taxa richness. To summarize the feeding guild structure, the abundance, percent of total abundance and number of taxa were calculated for each of the 5 feeding guilds (gatherers, scrapers, shredders, filterers, and predators).

3.2.2 Analysis

Invertebrate data was divided into two matrices: taxonomic and feeding guild. The taxonomic data were analyzed at the family level to reduce the number of taxa occurring

in only one site. Invertebrate families occurring in only one site were also removed resulting in 40 taxonomic groups used in analyses.

Ordinations by correspondence analysis were performed to determine how much of the variation in both sets of invertebrate community data could be explained by variables at each of the 3 spatial scales (local, riparian, and catchment). Data were analyzed including all sites (23), with only the small RCA sites (n=12), and with only the large RCA sites (n=11) for a total of 18 ordinations. Canonical correspondence analysis (CCA) was used on the taxonomic invertebrate data and redundancy analysis (RDA) was used for the feeding guild metric data. The feeding guild metric data was analyzed using the monotonic model (RDA) rather than the unimodal model (CCA) based on ordination axes being less than 2 SD in preliminary CCA ordinations suggesting monotonic response curves (Jongman et al. 1987). All ordinations were performed in CANOCO 4.5 (Biometris, Wageningen, The Netherlands) using inter-species relationships and bi-plot scaling. In CCA the taxonomic data were log transformed and rare species downweighted. In RDA the feeding guild metrics were divided by standard deviation, centered and not transformed.

Multiple response permutation procedure (MRPP) and non-metric multidimensional scaling (NMS) were used to determine differences in stream habitat characteristics and invertebrate communities between RCA classes (PC-ORD, MjM Software, Gleneden Beach, Oregon, U.S.A.). The NMS ordinations were all done using the Bray-Curtis

distance measure and PC-ORD slow and thorough autopilot including 250 runs in 6 dimensions.

To determine the relative strength of associations of the riparian and catchment scale landscape variables with invertebrate communities, ordinations were done for invertebrate data and combined riparian and catchment scale variables, for both small RCA sites and large RCA sites. Analysis was done on both taxonomic and feeding guild data for a total of 4 ordinations.

To determine the effects of harvesting on invertebrate communities, MRPP was used to determine if there was a significant difference in invertebrate community between reference and harvested sites. MANOVA was used to distinguish the specific effects of RCA size, harvesting and interaction effects on the abundance and richness of taxonomic groups and feeding guilds (SPSS 16.0.1, SPSS Inc, Chicago, Illinois).

3.3 RESULTS

3.3.1 Invertebrate community

A total of 18 435 invertebrates were collected and identified (Appendix I). After removing 15 taxa occurring in only one site, 40 taxa (at family level classification) were included in the analyses. The family Chironomidae was dominant in almost all sites comprising 63% of all individuals. The Simuliidae (black flies) were the next most dominant taxa comprising approximately 14% of all individuals. The communities were dominated by the filter feeding (29-49%) and gatherer (21-48%) feeding guilds.

3.3.2 Invertebrate-environment relationships

Canonical correspondence analysis (CCA) and redundancy analysis (RDA) ordinations both indicated that variation in invertebrate community structure was most strongly associated with local and catchment scale variables. The CCA analysis of invertebrate taxa showed that variables at the local, riparian and catchment scales explained 51.6%, 40.3%, and 43.9% of among-site variation in invertebrate taxonomic composition respectively. Only ordinations based on local and catchment scale variables had all axes significantly different from a random configuration (Monte Carlo randomization test, $p=0.002$ and $p=0.036$ respectively). The RDA analysis of invertebrate feeding guilds showed a similar pattern with local, riparian, and catchment scale variables explaining 59.1%, 37.5%, and 43.5% of among-site variation in feeding guild composition respectively. Only the ordination based on local variables had all axes significantly different from random ($p=0.048$).

An RDA ordination of feeding guilds and local scale habitat variables showed two roughly orthogonal gradients of local habitat characteristics; a depositional gradient (from slower streams with greater % fine substrate, to greater velocity and more coarse substrate) and a temperature gradient (from high water temperature to cooler water with greater DO). Sites dominated by filter feeders were most closely correlated with velocity, and sites dominated by gatherers and shredders tended to be correlated with fine substrate and higher water temperature (Fig 3.1a). An ordination of feeding guilds and riparian scale variables again showed two roughly orthogonal gradients of riparian scale variables. Sites with a high abundance of shredders were correlated with greater tree

density contrasting with sites with high abundances of gatherers and filterers which were correlated with a greater proportion of the RCA harvested in the past 10 years. The second gradient separated sites with high abundance of scrapers which were correlated with greater topographic relief (CV elev) from sites with a greater abundance of filterers which were correlated with a higher proportion of bedrock in the RCA (Fig 3.1b). In the third RDA ordination of feeding guild structure and catchment scale variables the gradients of catchment scale variables separated sites based on topography and retention in wetlands. High abundances of shredders, scrapers and predators were correlated with greater topographic relief within the catchment and sites with high abundances of filter feeders were correlated with a greater proportion of wetlands in the catchment. Sites with greater abundances of gatherers also tended to be correlated with larger catchment size (Fig. 3.1c).

3.3.3 Reach contributing area effects

Local stream habitat differed significantly between RCA size classes (MRPP, $A=0.033$, $p=0.030$). An NMS ordination of sites based on local stream characteristics summarized 82% of the variability among sites (61% in axis 2 and 21% in axis 3; Fig. 3.2). The NMS ordination showed a separation between some large RCA sites and the small RCA sites along axis 2, and showed that sites were most strongly separated along a gradient associated with substrate size. The proportion of silt and sand, and amount of detritus were most strongly correlated with the negative end of axis 2, associated with large RCA sites, and proportion of coarse substrates (bedrock, boulder, cobble, and pebble) were most strongly correlated with the positive end of axis 2, associated with small RCA sites.

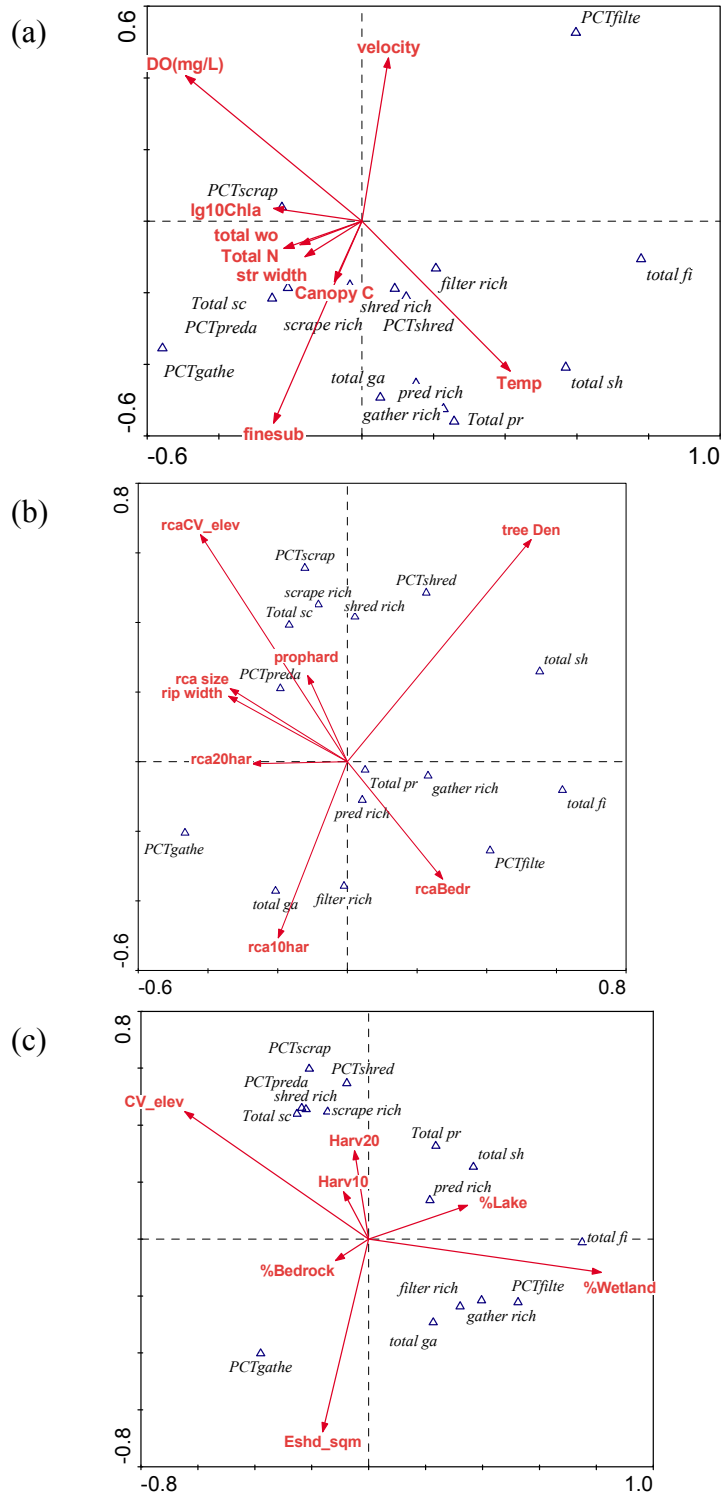


Figure 3.1. RDA ordinations showing axes 1 and 2 for all sites of invertebrate feeding guilds (points) and environmental variables (vectors) at (a) local scale, (b) riparian scale, and (c) catchment scale. Feeding guild abbreviations are comprised of PCT=%, rich=richness, total=abundance, ga=gatherer, fi=filterer, sh=shredder, sc=scrapper, and pred=predator.

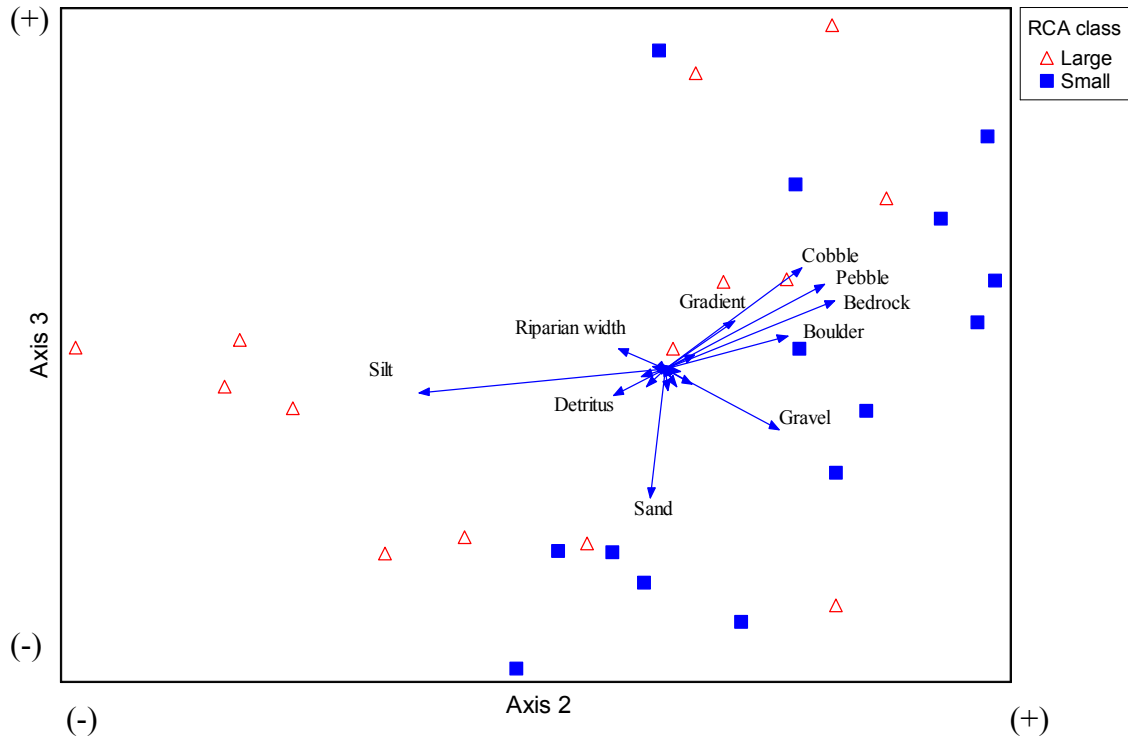


Figure 3.2. Non-metric multidimensional scaling of all sites based on local habitat characteristics using the Bray-Curtis distance measure. Large RCA sites are shown as triangles, Small RCA sites are shown as squares and the environmental variables are shown as vectors pointing in the direction of greatest correlation with the axes. Longer vectors represent stronger correlations with the axes. (Axes 2 and 3 capture 61% and 21% of among site variance respectively)

The stream gradient was also correlated with the positive end of axis 2, showing a trend for small RCA sites to be steeper and dominated by coarse substrate (erosional) while large RCA sites tended to have a shallower gradient and were dominated by fine substrate and detritus (depositional).

There was a significant difference in the composition of invertebrate communities between RCA groups (MRPP, $A=0.013$, $p=0.009$). An NMS ordination of all sites based on invertebrate taxa captures 43.7% of among site variation in invertebrate taxonomic structure in axes 2 and 3 (26.3% of in axis 2 and 17.4% in axis 3; Fig. 3.3). The separation of invertebrate communities between large RCA sites and small RCA sites was evident along axis 3. Sites at the negative end of axis 3 tended to have small RCAs and were dominated by filter feeding taxa, including Simuliidae, Hydropsychidae and Philopotamidae, predaceous taxa including Rhyacophilidae and the scraper taxon Glossosomatidae. Sites at the positive side of axis 3 tended to have large RCAs and were dominated by gatherer and shredder taxa from the Ephemeroptera (Ephemerellidae, Siphonuridae, and Leptophlebeidae), and Lepidoptera (Pyralidae). Small RCA sites had a higher proportion of Simuliidae and Plecoptera and a lower proportion of Oligochaeta and Nematoda (Fig. 3.4a,b). These taxa reflect differences in the dominant feeding guilds with large RCA sites dominated by gatherers, compared to a larger proportion of filter feeders in the small RCA sites (Fig. 3.4c,d).

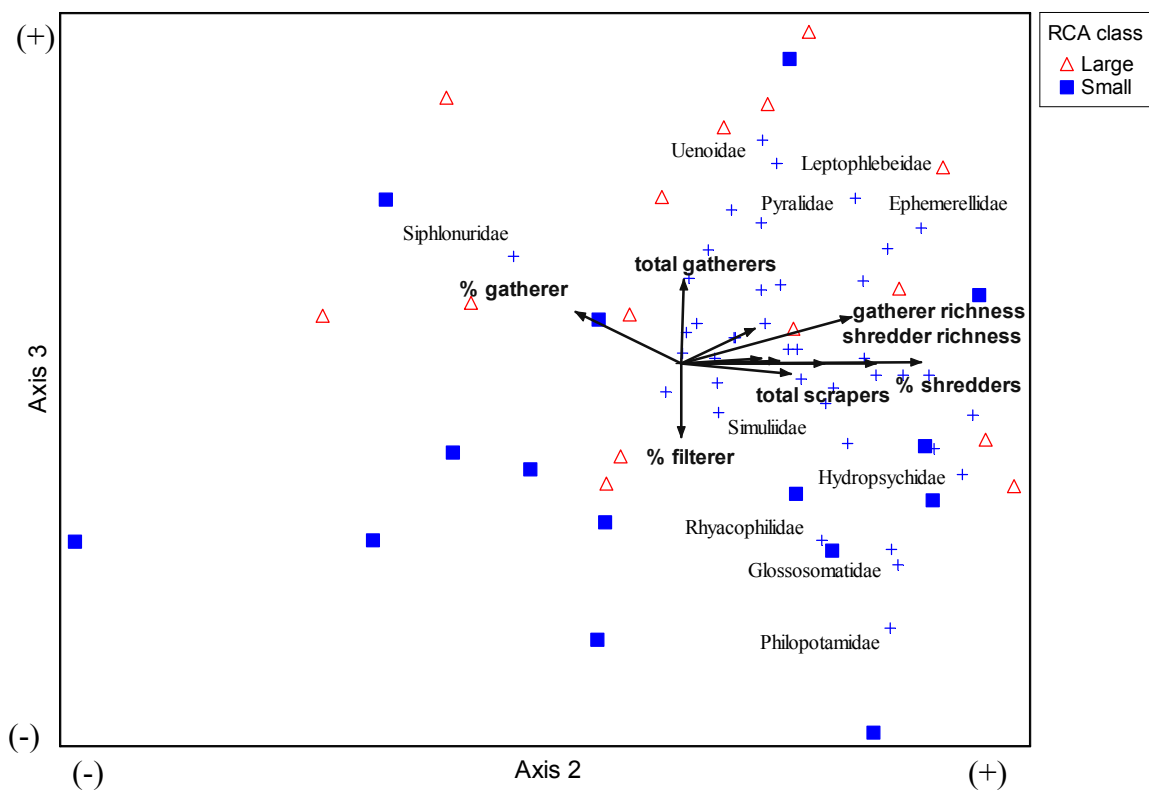


Figure 3.3. NMS ordination of all sites based on invertebrate taxonomic data using the Bray-Curtis distance measure. Triangles indicate large RCA sites, squares indicate small RCA sites. Crosses indicate invertebrate taxa and vectors indicate the correlation of feeding guild metrics with the axes (cutoff at a minimum correlation of $r^2=0.15$). (Axis 2 and 3 capture 26.3% and 17.4% of variation in invertebrate community respectively.)

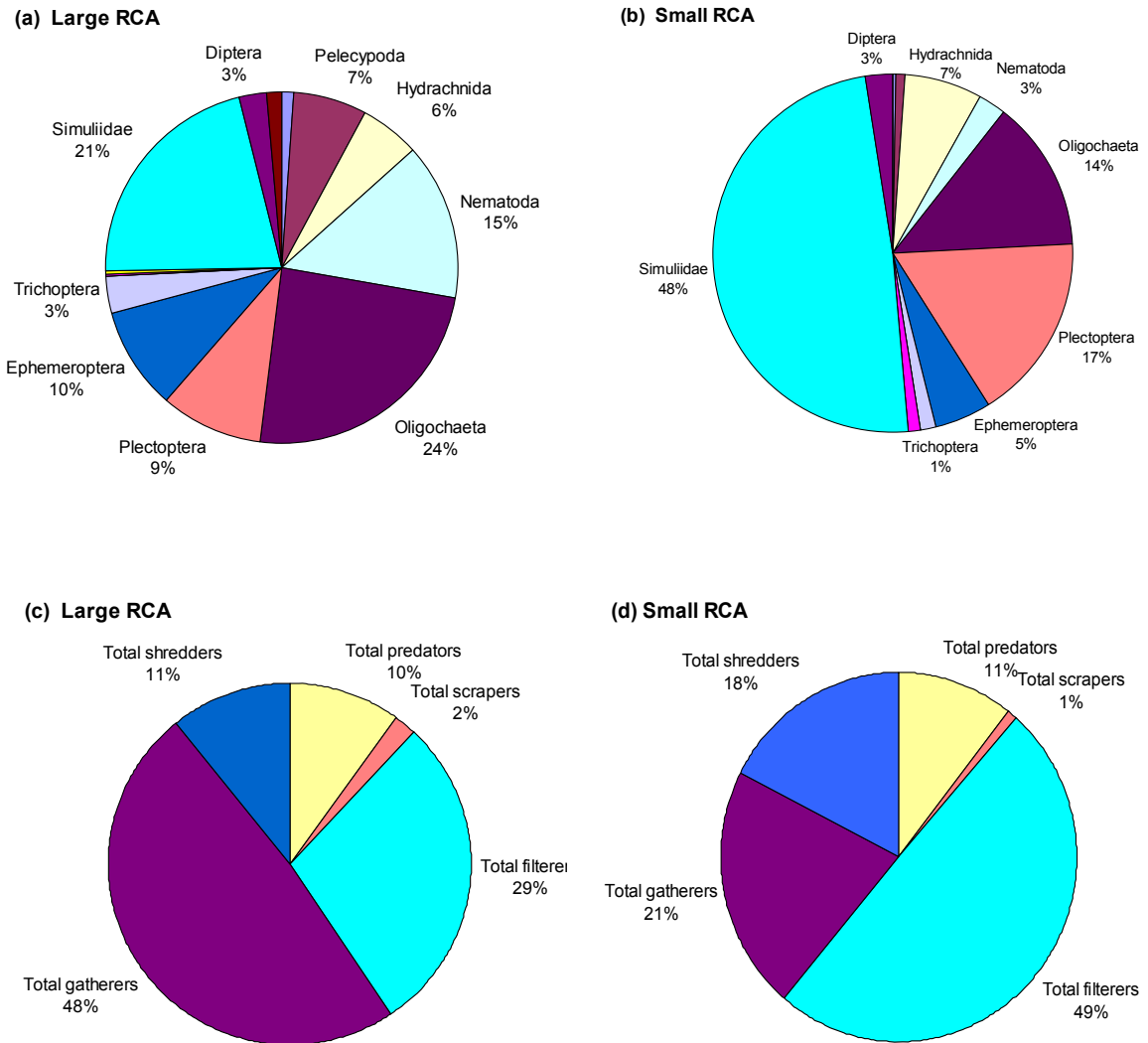


Figure 3.4. Average proportion of invertebrate orders (including Simuliidae at family level) in sites with (a) large RCAs and (b) small RCAs and feeding guilds in sites with (c) large RCAs and (d) small RCAs. The proportion of the family Chironomidae was excluded from the taxonomic data presented here to prevent their overall dominance from obscuring relevant patterns.

Local scale variables explained the most among-site variation in invertebrate community in both taxonomic and feeding guild data. Riparian and catchment scale variables explained approximately equal proportions of the variation in invertebrate taxonomic composition within small RCA sites, but in large RCA sites the riparian scale explained almost 10% more variation in invertebrate taxonomic composition than the catchment scale variables (Fig. 3.5a). The riparian and catchment scales had approximately equal explanatory power of feeding guild variation in large RCA sites, but in small RCA sites the catchment scale explained almost 23% more among-site variation in feeding guild composition than the riparian scale variables (Fig. 3.5b).

The RDA ordinations of feeding guild composition and combined riparian and catchment scale variables showed which variables were contributing to the relative explanatory strength of each spatial scale. In small RCA sites, 3 of the 4 variables most correlated with among-site variability in feeding guild structure were from the catchment scale. Tree density (riparian scale) was correlated most with sites dominated by the gatherer feeding guild, % bedrock in the catchment was most closely correlated with sites dominated by shredders, and % of the catchment harvested in the past 10 years was correlated with sites dominated by filterer feeders. The catchment size was negatively correlated with tree density, and therefore gatherers and predators were more often found at sites with high tree density (Fig. 3.6a). In large RCA sites 3 of the 4 variables most correlated with variability in feeding guild structure were from the riparian scale. Relief ratio in the RCA (rcaCV elev) and tree density were most correlated with sites dominated

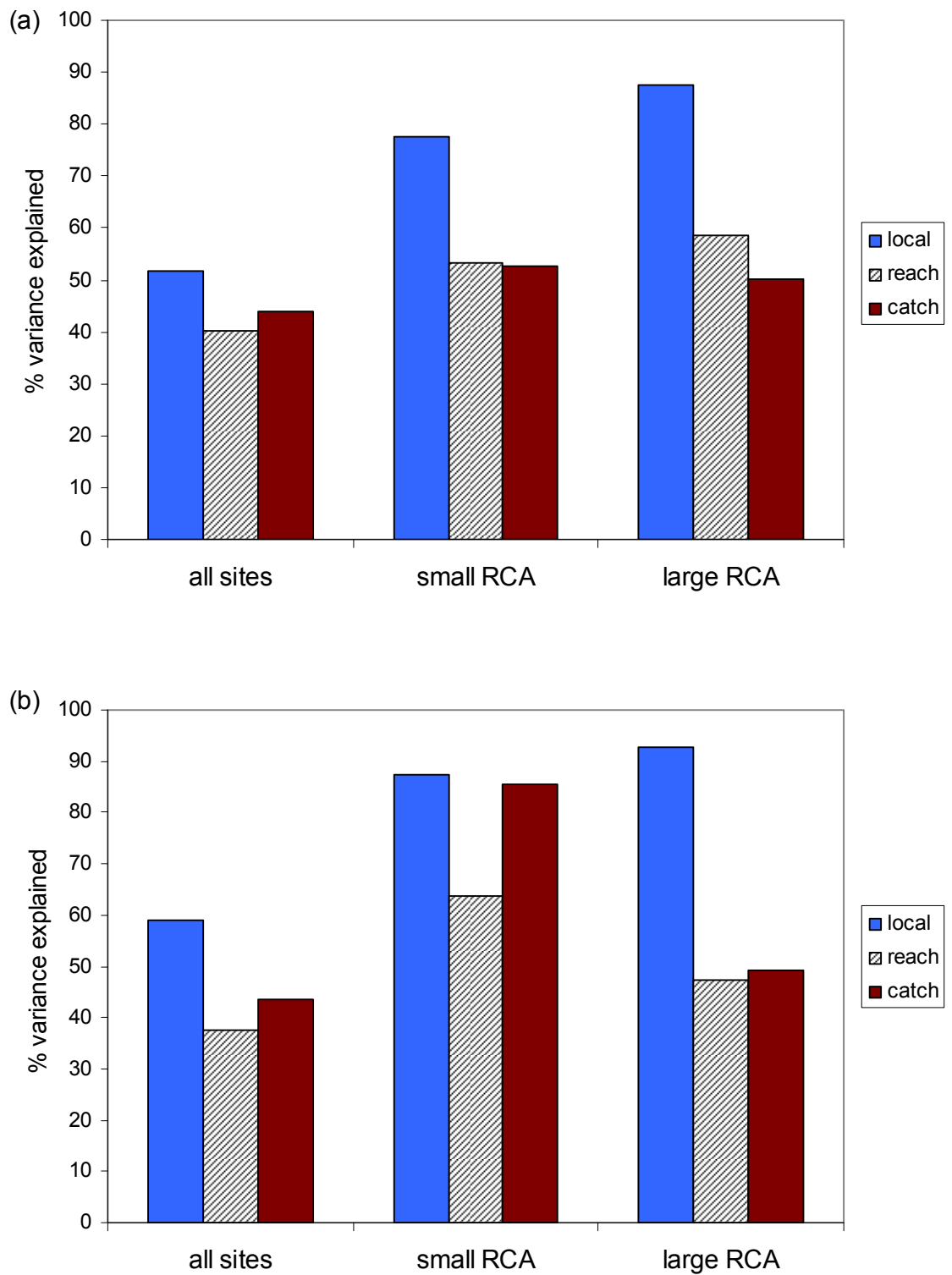


Figure 3.5. Relative contributions of environmental variables at the local, riparian, and catchment scale to explain variance of (a) invertebrate taxonomic composition and (b) feeding guild composition from CCA and RDA analyses (Appendix II)

by predators, scrapers and shredders. Bedrock in the RCA was correlated with sites dominated by filter feeders and % wetland (catchment scale) was correlated with sites dominated by gatherers (Fig. 3.6b).

3.3.4 Harvesting Effects

Total abundance and richness of invertebrate taxa differed significantly between harvested and reference sites. There were more than twice as many individuals on average at harvested sites than at reference sites ($F_{1,26} = 8.97$; $p = 0.006$; Fig. 3.7a), and almost 50% more taxa at harvested sites (average 14 taxa) than at reference sites (average 10 taxa) ($F_{1,26} = 7.13$; $p = 0.013$; Fig. 3.7b). MANOVA analysis showed which taxa had significantly higher abundances in harvested sites than in reference sites (Fig3.8):

Oligochaeta ($F_{1,26} = 4.28$, $p = 0.049$), Pelecypoda ($F_{1,26} = 4.47$, $p = 0.044$), Chironomidae ($F_{1,26} = 5.44$, $p = 0.028$), Heptageniidae ($F_{1,26} = 7.15$, $p = 0.013$), Hydropsychidae ($F_{1,26} = 7.69$, $p = 0.010$), Polycentropodidae ($F_{1,26} = 8.24$, $p = 0.008$), Philopotamidae ($F_{1,26} = 11.09$, $p = 0.003$), Elmidae ($F_{1,26} = 22.82$, $p < 0.001$) and Hydrachnida ($F_{1,26} = 12.37$, $p = 0.002$). Increased taxonomic richness is reflected by a significantly higher number of taxa in filter feeders and scrapers, and nearly significant differences in predators and gatherers (on average 1 more taxon in harvested sites than reference sites; scrapers $F_{1,26} = 25.81$, $p < 0.001$; filterers $F_{1,26} = 25.07$, $p < 0.001$; predators $F_{1,26} = 3.60$, $p = 0.069$; gatherers $F_{1,26} = 3.26$, $p = 0.082$; Fig. 3.9).

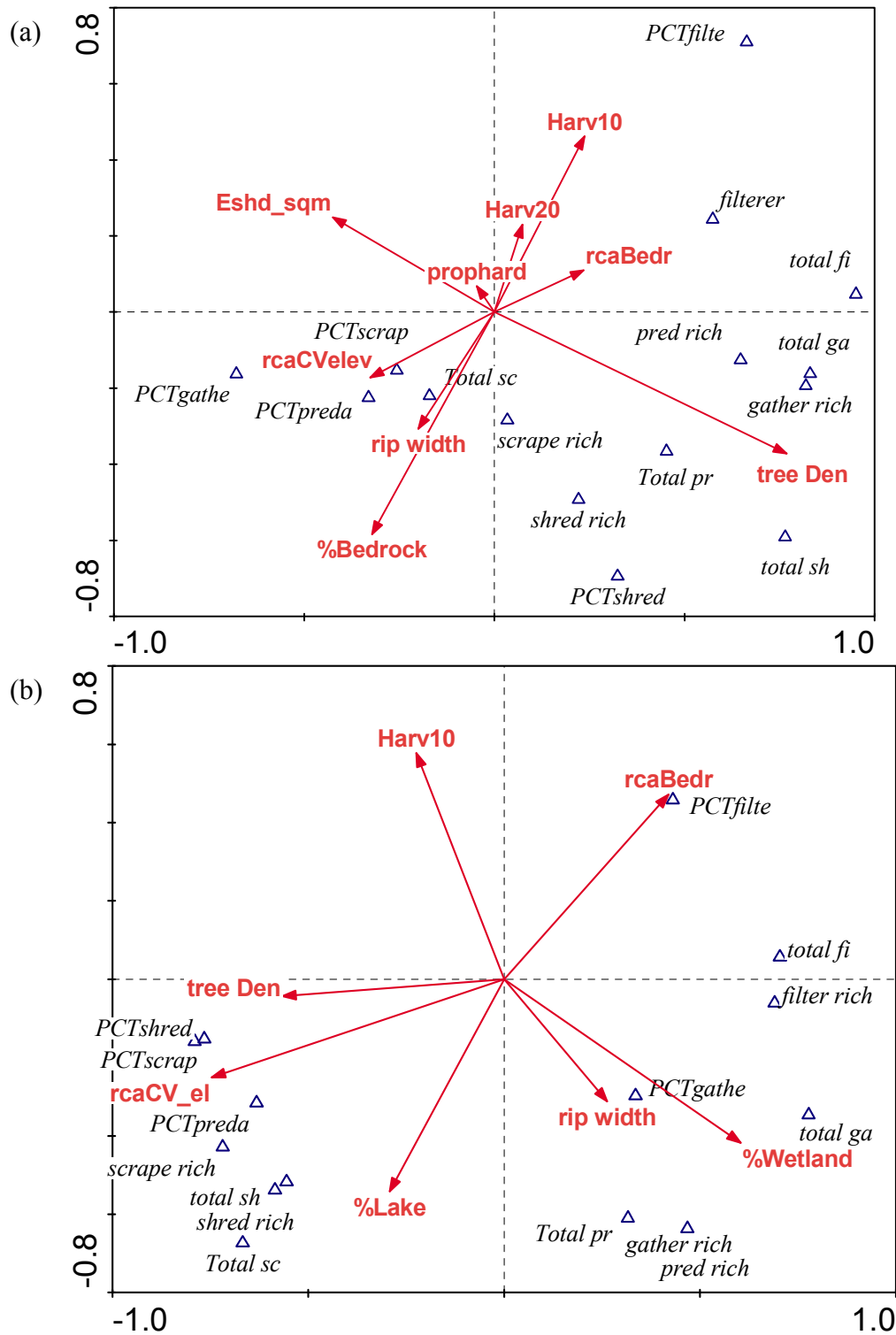


Figure 3.6. RDA ordinations (axes 1 and 2) of invertebrate feeding guild composition (points) and landscape variables (vectors) at the riparian, and catchment scale in sites with (a) small RCAs and (b) large RCAs

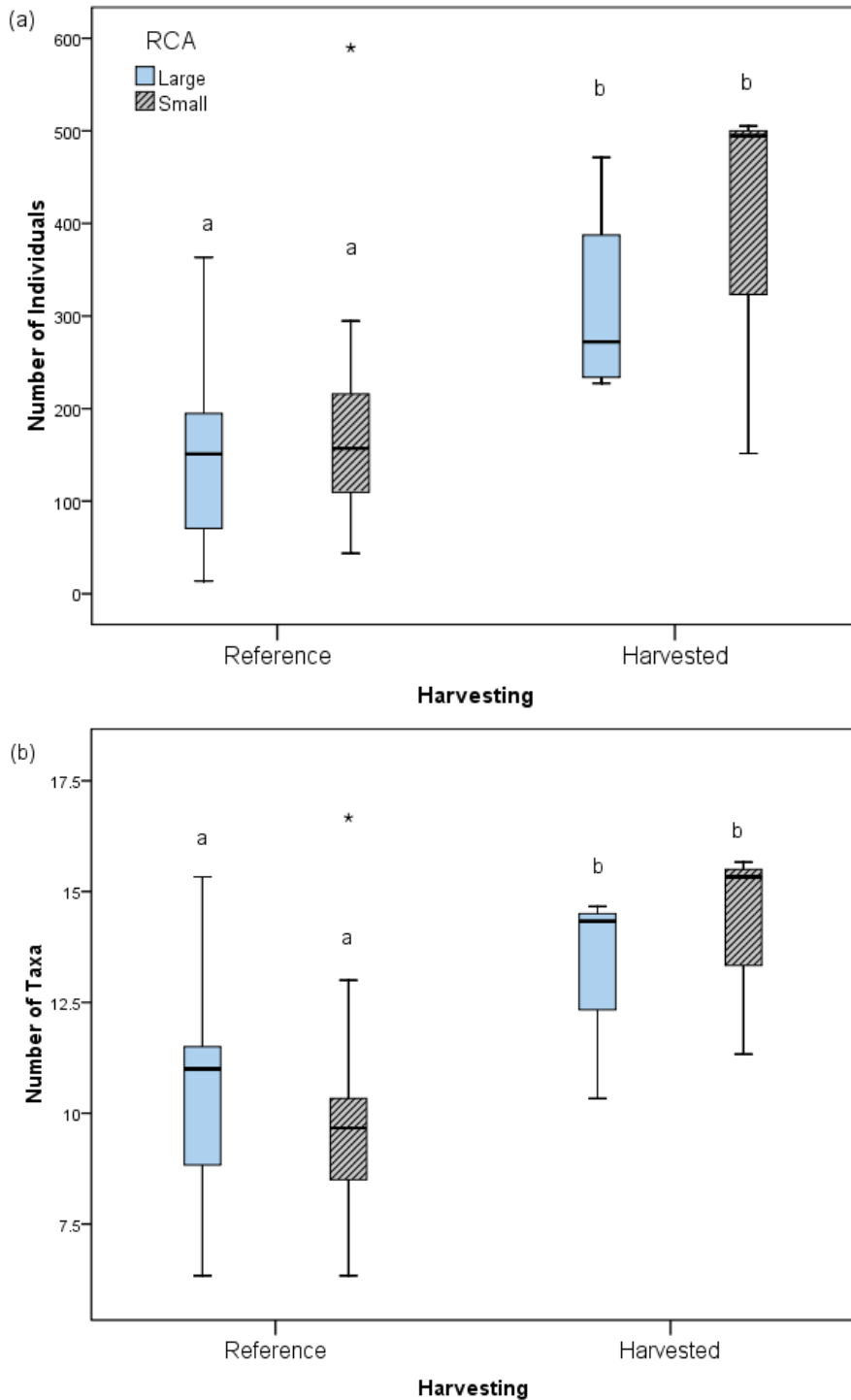


Figure 3.7. Boxplots of (a) average abundance and (b) average richness in reference sites (left boxes) and harvested sites (right boxes). Boxes are shown for large RCA sites (solid) and small RCA sites (striped). Solid line represents median, boxes represent inter-quartile range, and whiskers indicate the range. Asterisks denote outliers >3 SD from median. Different letters denote significant differences in means determined by a MANOVA with RCA and harvesting as factors.

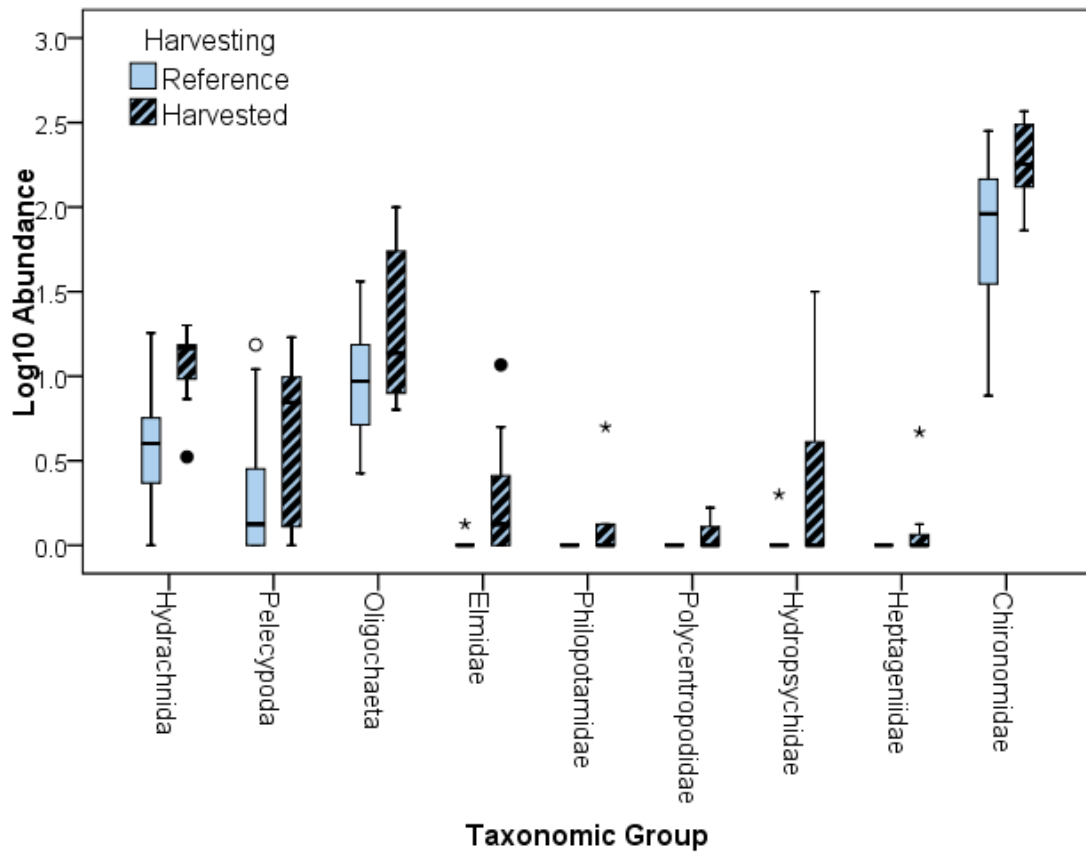


Figure 3.8. Boxplots of \log_{10} mean abundance of invertebrate taxa with significant differences between reference and harvested site. All taxa shown differ significantly between reference and harvested sites (MANOVA $p < 0.05$). In boxes, solid line represents median, boxes represent inter-quartile range, and whiskers represent the range. Open circles and asterisks represent outliers > 3 SD from median.

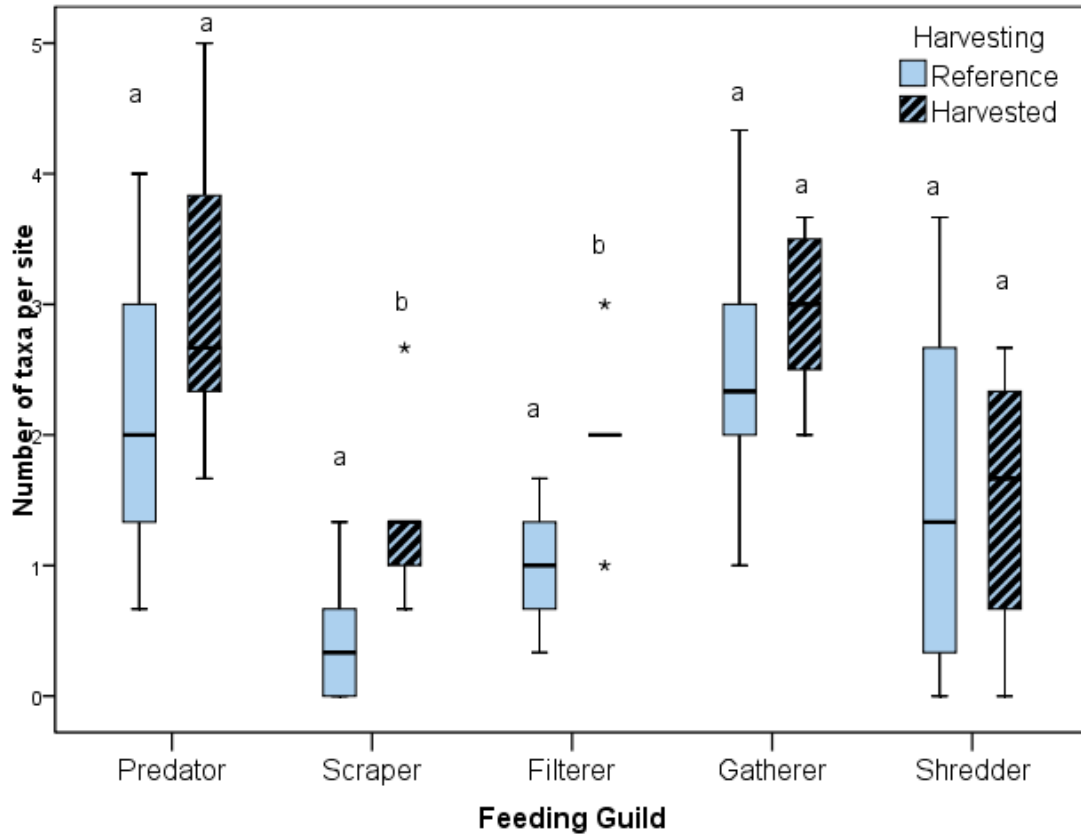


Figure 3.9. Boxplots of square root transformed richness within each feeding guild in reference and harvested sites. Different letters above boxes (a, b) denote significant differences between reference and harvested sites (MANOVA $p < 0.05$). In boxes, solid line represents median, boxes represent inter-quartile range, and whiskers represent the range. Asterisks represent outliers > 3 SD from median.

Table 3.1. Summary of MANOVA results for invertebrate taxa and metrics showing significant interaction effects between harvesting and RCA size

Family or metric	Harvesting Effect		F	p
	Large RCA	Small RCA		
Scraper richness	2x greater in harvested sites	5x greater in harvested sites	5.60	0.020
% EPT	No difference	2x greater in harvested sites	4.25	0.042
EPT richness	No difference	2x greater in harvested sites	4.37	0.039
Capniidae	4x more in harvested sites	Zero in harvested sites	4.28	0.049
Rhyacophilidae	Zero in harvested sites	7x more in harvested sites	5.80	0.023
Philopotamidae	No difference	From zero in reference to 1.5 in harvested	7.02	0.014
Dytiscidae	Greater in harvested sites	Less in harvested sites	6.38	0.018
Elmidae	No difference	From zero in reference to 4.8 in harvested sites	14.79	0.001

An MRPP of invertebrate taxa between reference and harvested sites showed a significant difference in composition of the two groups ($A = 0.026$, $p = 0.011$). Several families in the Ephemeroptera (Ephemerellidae, Heptageniidae), Trichoptera (Hydropsychidae, Polycentropodidae, Philopotamidae, and Leptoceridae) and Coleoptera (Elmidae, Scirtidae) were found only in harvested sites.

There were some interaction effects between RCA and harvesting on richness and abundance (see table 3.1 for significant taxa and metrics with statistics), however when considering both RCA and harvesting factors, sample sizes for each category are very low ($n = 3$ for harvested small RCA sites and $n = 4$ for harvested large RCA sites) so it is not possible to draw conclusions confidently. The tendency is for small RCA sites to show a greater difference in invertebrate community between reference and harvested sites than large RCA sites.

3.4 DISCUSSION

3.4.1 Invertebrate - environment relationships

I found that factors at the local habitat scale explained the most variation in the invertebrate community. Studies of factors at multiple spatial scales often state that patterns of invertebrate assemblage can only be sufficiently explained by combining all spatial scales (Brosse et al. 2003; Corkum 1989; Weigel et al. 2003). Other studies of multiple spatial scales have identified the importance of local habitat scale in structuring invertebrate communities (Brosse et al. 2003; Sponseller et al. 2001), the lack of explanatory power of catchment scale variables (Heino et al. 2008; Hawkins and Vinson

2000) and the relative importance of intermediate riparian scale variables (Feld and Hering 2007). These contradictory results may reflect the complex interactions between spatial scales (Frissell et al. 1986) or the measure of in-stream community being used. Weigel et al. (2003) found that the relative importance of spatial scales varied depending on the type of invertebrate data being explained (invertebrate metrics, relative abundance, or presence/absence). The relatively greater importance of local habitat scale as opposed to catchment scale factors in this study may be explained by the relatively small geographic area over which the study was conducted. By contrast, studies over large areas often find the largest spatial scale to be most associated with differences in invertebrate community (Corkum 1992).

Substrate has been shown to be important in structuring invertebrate communities due to surface area for colonization and algal growth, alteration of water currents, and the ability to sequester detritus particles (Rabeni and Minshall 1977). Water velocity has also been shown to be an important habitat characteristic (Corkum 1989) which can be related to substrate particle size (Allan, 1995), and food resources such as periphyton growth (McIntire 1968) and organic detritus (Habdija et al. 2004). In this study, detritus was highly correlated with fine substrate ($R^2 = 0.519$, $p < 0.001$) which was one of the local variables most strongly associated with invertebrate community variation, and was therefore omitted from ordination analyses but may still be an important factor. The dominant feeding guilds were distributed along a depositional gradient providing either more detritus (gatherers), or more suspended fine organic particles (filterers) (Cummins and Klug 1979). Temperature was another local variable strongly correlated with

invertebrate community structure, and has been known to affect metabolism, assimilation efficiency and life cycle timing (Vannote and Sweeney 1980) which can play a role in feeding guild dominance and community assemblage.

Riparian scale variables explained the least variation in invertebrate community composition but still explained more than a third of the variation. The strongest correlation at the riparian scale was between sites dominated by scrapers and greater topographic relief in the RCA. In the boreal shield, the soil layer is shallow and bedrock is prominent. In areas with high topographic relief, there may be greater potential for accumulation of deeper soils and for subsurface water flow (as shown in the negative correlation between topographic relief and bedrock forms). It has been shown in models of stream geomorphology that changes in slope and retention areas (e.g. hyporheic zones) in stream reaches can increase nutrient retention and algal biomass (Doyle and Stanley 2006). The greater potential for periphyton growth at these sites could explain the higher abundance of scrapers.

Sites dominated by the shredder feeding guild were most correlated with high tree densities in the RCA, presumably due to greater potential for leaf input to the stream (Cummins and Klug 1979). Conversely, sites with the most harvesting in the past 10 years supported greater populations and relative abundance of gatherers and filterers. This may be due to persisting effects of increased particulate organic material being mobilized by past harvesting and transported (at least in large RCAs) by unmapped surface streams. Alternatively, the invertebrate community could be responding to

increased dissolved organic material inputs resulting from a correlation between 10 year harvesting, and lower topographic relief in the RCA. These feeding guilds were also correlated with proportions of lakes and wetlands in the catchment which could be influential, as discussed below. In another study on low-order boreal streams the opposite trend was found; gatherers and filterers relying on fine particulate organic matter were less abundant in clear-cut areas as a result of lower leaf decomposition in those areas (Kreutzweiser et al. 2008). These differences may be a result of the larger streams being studied by Kreutzweiser (up to 4th order streams, while on the same classification scale, the streams in my study are 0 or 1st order streams) which may support a different invertebrate community based on original stream habitat.

Topographic relief has been shown to affect stream habitat and invertebrate community on several scales (Brosse et al. 2003; Montgomery 1999). Increased relief ratio created more heterogeneity in the stream habitat which supported a greater richness of species. In this study, greater relief ratio was not associated with sites with greater richness in every feeding guild however, sites dominated by shredders, scrapers, and predators were correlated with greater topographic relief. This may be explained similarly to the riparian scale association: variation in geomorphology may create more water storage areas, resulting in more nutrient retention and more algal growth (Doyle and Stanley 2006) which may support more scrapers. At the other end of the gradient, a greater percentage of wetlands in the catchment was correlated with sites dominated by grazers and filterers relying on fine particulate organic material. Organic matter accumulating in wetlands has a high rate of decomposition (Bayley et al. 1985) which would result in coarse organic

material being reduced to fine particulate organic matter. Repeated flooding in the fall and spring in the Nipigon forest area may result in flushing of the fine particulate organic material from the wetlands into streams to support a greater population of filter feeders and gatherers.

Catchment size has long been used to predict the invertebrate community and the associated characteristics of increasing catchment size is well understood (Vannote et al. 1980). The size of the catchment for each stream site was kept small in this study, although because sites were chosen in streams with a catchment range of 46 to 146 hectares, the size of the catchment did have an effect on invertebrate community. Generally in larger streams, there is less leaf litter input from the riparian zone, and therefore relatively more fine particulate organic matter contributed from upstream. Collectors (filterers and gatherers) should then be the dominant functional groups in larger streams (Vannote et al. 1980), which is indeed what I found in stream sites with larger catchment areas.

3.4.2 Reach contributing area effects

Montgomery (1999) states that while watershed conditions may form a continuum over large spatial scales, at small spatial scales geomorphic and topographic controls create a mosaic of different ‘process domains’. I have, indeed, found that at the scale of variation within headwater streams which tend to be classified as a single functional unit, topographic controls created reaches with different stream conditions and biotic communities. The invertebrate community differed between small and large RCA size

classes based on differences in the dominant feeding guild. Filter feeders tended to be dominant in sites with small RCAs driven by a higher abundance of Simuliidae, while sites with large RCAs tended to be dominated by the gatherer feeding guild, driven by greater abundances of Oligochaetes and Ephemeroptera. These patterns of invertebrate assemblages seem to be associated with inherent morphological differences in the streams based on topographic controls. Small RCA sites were steeper with larger substrate particles, while large RCA sites had a shallower gradient dominated by fine substrate and detritus. This separation into erosional and depositional habitats is a fairly reliable predictor of general functional group assemblages (Merritt and Cummins 1996; Vannote et al. 1980; Montgomery 1999).

Analysis of the relative contributions of variables at each spatial scale shows a trend for riparian scale variables to be relatively more important at large RCA sites, and catchment scale variables to be relatively more important at small RCA sites. Studies of the link between hillslope processes and stream conditions indicate that at a large scale, wide, flat valleys tend to be disconnected from hillslope processes due to greater buffering capacity of the riparian zone, and streams with steep valley sides will be more strongly affected by those hillslope inputs (McGlynn and Seibert 2003; Montgomery 1999). My results do not support this pattern, which could be an effect of the scale of variation being studied. Most studies of this nature focus on variation from headwater streams to larger downstream reaches, whereas my study is focused on variation at a much smaller spatial scale within headwater streams. The proposal that disturbance on steep slopes will have a stronger effect on streams due to less buffering capacity of the riparian zone

(Montgomery 1999) is not applicable to my sites where the steep banks only extend to a maximum of 30m from the stream, where a ridge separates the stream from the rest of the upland contributions.

The difference in the relative importance of riparian and catchment spatial scales may be explained 2 ways. The first explanation is based on the process domains theory in which topography separates stream reaches based on disturbance effects (Montgomery 1999). Montgomery (1999) states that steep channels constrained by steep banks (a small RCA in my study) will be more affected by flood disturbance (by scouring, for example) whereas low gradient channels with extensive floodplains (a large RCA in my study) will be less affected by flooding as they can expand into the floodplain. Arscott et al. (2005) have also shown how connectivity with the floodplain can affect the macroinvertebrate community of the stream reach. This may be mediated through differences in groundwater and nutrient exchange between the floodplain and the stream waters. Both of those factors could be affected by the bedrock and topographic relief in the RCA, which are strongly associated with invertebrate community in large RCA sites in this study.

The second explanation could be that in my study system a physical barrier to lateral inputs may exist in the small RCA sites. Small RCA sites were characterized by steep banks culminating in a ridge close to the stream. These ridges could effectively block any lateral inputs from soil or vegetation from reaching the particular stream reach, thereby reducing the importance of those lateral variables in structuring the invertebrate

community. In this case, most of the input to the stream will be in the form of longitudinal flow which has been influenced by factors in the entire catchment, such as bedrock and historical harvesting. This interpretation would only be applicable to similarly bedrock-dominated landscapes in which the bedrock forms can be predicted by surface topography.

My study illustrates that landscape effects on aquatic habitats act at a small scale within headwater streams. A better understanding of how invertebrate communities are linked to the surrounding landscape and topographic controls on those linkages may lead to more effective conservation and management of small streams and the biotic communities that are essential to the functioning of the watershed.

3.4.3 Harvesting effects

All harvested streams in this study were protected by a forested riparian buffer at least 30m wide. Buffers have been shown to effectively protect the aquatic community from effects of forestry when compared to sites harvested without a buffer (Newbold et al. 1980; Moldenke and Ver Linden 2007). This study shows a marked contrast to those results with considerable increases in both abundance and richness in buffered harvested sites. Increased abundance and biomass in harvested stream sites is generally attributed to an increase in primary production due to more light penetrating the canopy (Kiffney et al. 2003) and increases in deciduous leaf litter inputs (Whiles and Wallace 1997) due to early successional species replacing mature coniferous forest. In this study, the amount of chlorophyll *a* and the proportion of hardwood did not increase in harvested sites,

however the stream temperature and nitrogen concentration did increase significantly (see section 2). The increases in temperature and nutrients agrees with much of the published literature, however the lack of increase in chlorophyll *a* leaves out the mechanism for the increased invertebrate abundance. It is possible that the difference in temperature is directly affecting invertebrate reproduction and life cycles (Vannote and Sweeny 1980). The short period over which this study was conducted may contribute to the lack of effects shown in chlorophyll *a*. It may be that samples taken closer to the end of the growing season may show differences in periphyton growth in harvested sites.

The invertebrate taxa with significantly higher abundances in harvested stream sites tend to have higher tolerances to warm temperatures and low oxygen levels. The caddisflies Polycentropodidae and Hydropsychidae, the mayfly Heptageniidae and the dipteran Chironomidae are all common in lentic habitats such as the littoral areas of lakes or shallow temporary ponds which would have much lower O₂ levels than flowing cold water streams. Polycentropodidae and the riffle beetle, Elmidae, can both adapt to low oxygen environments by creating water currents through a tube, or 'pumping' their gills respectively (Hilsenhoff 1991). The Oligochaeta are also common in habitats with soft sediment and have a wide range of tolerance to low O₂ and pollution.

Increased richness of most feeding guilds in harvested areas could be the result of an increase in food supply which would support a greater number of species. Increases in surface runoff from harvested areas (Steedman 2000) can bring greater inputs of particulate organic material into the stream to support filter feeders and gatherers.

Theoretically, scrapers would respond to an increase in periphyton growth due to increased stream temperature and nutrients, however I did not observe an increase in periphyton at harvested sites. The increased scraper richness could be a result of increases in non-autotrophic microbes due to higher temperatures (Merritt and Cummins 1996). Greater predator richness can be supported by increased abundance of prey individuals in general. Shredder richness did not differ between reference and harvested areas. The effect of clear-cut harvesting on the shredder feeding guild is not well resolved. Nislow and Lowe (2006) found that shredders decreased after harvesting, due to the removal of deciduous canopy in a New England stream. Conversely, Stone and Wallace (1998) found an increase in shredders which they linked in increases in herbaceous leaf inputs during early successional stages after harvesting. The consistency in shredders in this study may be due to the retention of treed buffers around the stream at harvested sites, and the dense stands of speckled alder in riparian zones which can provide a constant source of coarse organic matter into the stream. Differences in invertebrate community may also be a result of correlations with low topographic relief and wetlands in the catchment as discussed in section 2.

I found that all harvested sites showed differing macroinvertebrate communities and, contrary to my hypothesis, stream sites with a small RCA showed greater effects of harvesting than those with a large RCA. Due to small sample sizes when considering both RCA and harvesting factors, these results should be interpreted cautiously. I suggest that harvesting effects may be less pronounced at large RCA sites, despite the RCA being exposed to the clear-cut, due to stabilizing effects of the larger riparian area (see section

2). Increased nutrient flux and organic inputs from the clear-cut area into the stream may be mitigated through soil and plant uptake in the riparian zone, and increased water temperature due to light exposure and runoff from the clear-cut may be off-set by greater groundwater input. Stream sites with small RCAs may not have these direct lateral inputs, but any effects from nearby upstream lateral inputs cannot be mitigated in this way.

My first two hypotheses regarding invertebrate communities in relation to RCA size class were supported. The largest differences in invertebrate community were in the composition of the functional feeding guilds, and the invertebrate communities in stream reaches with large RCAs were more strongly correlated with lateral terrestrial area than those in reaches with small RCAs. These conclusions can give rise to several new hypotheses regarding mechanisms for these differences such as testing if there is a greater concentration of fine particulate organic matter being transported to stream reaches from large RCAs than at small RCAs. The hypothesis that more tolerant invertebrate taxa would increase in abundance at harvested sites was supported, but that result was perhaps overshadowed by the overall increase in abundance and richness of the community as a whole. My hypothesis regarding the magnitude of harvesting impacts on invertebrate communities being greater at large RCA sites was not supported. The impacts of harvesting were evident at stream sites with both large and small RCAs which could generate hypotheses regarding mechanisms for transport of runoff and materials produced by harvesting into buffered sites.

4.0 CONCLUSIONS

The results of this study characterize the variation in stream habitat, macroinvertebrate communities, and linkages with the terrestrial environment that occurs within headwater streams. Stream habitat varied from erosional characteristics with greater oxygen content to depositional characteristics with greater organic and nitrogen content. Primary productivity in streams was dependent on a combination of characteristics from both ends of the overall gradient. This variation created areas with mostly autochthonous sources of energy input and areas dependent on allochthonous input both within streams with a catchment areas of between 46 and 146ha. These results reveal variation in streams which are generally grouped together as a single functional group (Vannote et al. 1980).

The variation in stream habitat characteristics was associated with the terrestrial environment at different spatial scales. The terrestrial variables most associated with instream habitat variation were dependent on the local topography (RCA). I found that terrestrial characteristics at the riparian scale were always more closely associated with local stream habitat than catchment scale characteristics. This pattern was strongest at sites with large RCAs, with the riparian scale explaining 40% more variation in local habitat characteristics than could be explained by the catchment scale variables. The riparian scale variables most strongly correlated with local habitat were related to soils (riparian width and bedrock) which were linked with substrate, water temperature and nutrient composition. The strongest catchment variables were topographic (correlated with temperature and flow velocity) and lakes and wetlands in the catchment (correlated with temperature, organics, and nutrient composition). These different correlations

between spatial scales based on topography created different linkages between stream and terrestrial environments at reference and harvested sites, as a result of the general characteristics that make the areas suitable for harvesting. Harvested sites had significantly different local stream characteristics and different correlations with riparian scale variables. Stream habitat at harvested sites was more associated with variables related to forest cover, and reference sites were more associated with topographic variables at the riparian scale.

Benthic macroinvertebrate communities were a good indicator of stream habitat variation and of differences in aquatic-terrestrial linkages. Community composition differed between sites with large and small RCAs corresponding to differences between erosional and depositional habitats. Taxonomic and functional invertebrate structure was most closely associated with small scale, local instream habitat variables. The correlation with terrestrial variables at different scales was dependent on the size of the RCA and the attributes of the community being analyzed. In large RCA sites, the riparian scale variables had almost 10% more influence on taxonomic structure than catchment scale variables, and in small RCA sites catchment scale variables explained almost 23% more variation in feeding guild structure than riparian scale variables. Topographic relief was an important variable at both the riparian and catchment scales. Variables at the riparian scale most correlated with the invertebrate community tended to be related to forest cover whereas important variables at the catchment scale were related to topography, wetlands and lakes.

Macroinvertebrate communities were also found to vary based on harvesting disturbance. Sites with recent local harvesting had significantly higher abundances and richness of benthic invertebrates. Greater taxonomic richness was found in every feeding guild except the shredder guild. Significant differences in composition were also found based on greater abundances of invertebrate families which can tolerate higher temperatures and lower oxygen which was characteristic of harvested sites. The magnitude of differences in invertebrate communities tended to be greater in stream reaches with small RCAs, contrary to my hypothesis that large RCAs would be more susceptible to harvesting impacts.

The difference in correlations between stream habitat characteristics, invertebrate community structure, and terrestrial environmental factors based on RCA indicates the importance of local topography on the linkage between aquatic habitats and the surrounding terrestrial environment. Understanding the scale at which these linkages vary, and how that may affect aquatic biotic communities can help develop more effective conservation and management strategies for all habitats and processes present in small streams.

5.0 LITERATURE CITED

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APPENDIX I

Summary of all invertebrate taxa collected

ORDER	FAMILY	GENUS	Feeding Guild	Family total	Total	# of sites	
Plectoptera	unkn	<i>unkn</i>		15	15	5	
	Nemouridae	<i>unkn</i>	Shredders	451	4	2	
		<i>Nemoura</i>	Shredders		43	10	
		<i>Amphinemoura</i>	Shredders		404	12	
		Leuctridae	<i>Leuctra</i>	Shredders	190	190	15
		Capniidae	<i>Paracapnia</i>	Shredders	108	108	12
		Perlodidae	<i>Isoperla</i>	Predator	2	2	1
Ephemeroptera	unkn	<i>unkn</i>		21	21	7	
	Baetidae	<i>Baetis</i>	Gatherers	280	280	19	
	Leptophlebeidae	<i>Leptophlebia</i>	Gatherers	110	110	11	
	Siphonuridae	<i>Siphonurus</i>	Gatherers	16	16	4	
	Ephemerellidae	<i>Eurylophella</i>	Gatherers	2	1	1	
		<i>unkn</i>			1	1	
		Heptageniidae	<i>Heptagenia</i>	Scraper	12	12	2
Trichoptera	unkn	<i>unkn</i>		4	4	3	
	Hydropsychidae	<i>Hydropsyche</i>	Filter feeder	142	92	1	
		<i>Cheumatopsyche</i>	Filter feeder		50	2	
	Hydroptilidae	<i>unkn</i>		60	4	1	
		<i>Neotrichia</i>	Scraper		52	5	
		<i>Oxyethira</i>	Herbivore		4	2	
	Limnephilidae	<i>unkn</i>		30	7	4	
		<i>Frenesia</i>	Shredders		9	5	
		<i>Limnephilus</i>	Shredders		8	7	
		<i>Pseudostenophylax</i>	Shredders		1	1	
		<i>Onocosmoecus</i>	Shredders		2	2	
		<i>Halesochila</i>	Gatherers		1	1	
		<i>Clistoronia</i>	Gatherers		2	1	
		<i>Lepidostomatidae</i>	<i>Lepidostoma</i>	Shredders	33	33	11
	Polycentropodidae	<i>Polycentropus</i>	Predator	4	4	2	
	Rhyacophilidae	<i>pupa</i>		15	1	1	
		<i>Rhyacophila</i>	Predator		14	7	
	Philopotamidae	<i>pupa</i>		14	1	1	
		<i>Wormaldia</i>	Filter feeder		13	2	
		Glossosomatidae	<i>Glossosoma</i>	Scraper	18	18	3
		Uenoidae	<i>Neophylax</i>	Scraper	17	17	2
		Leptoceridae	<i>Setodes</i>	Gatherers	1	1	1
	Lepidoptera	unkn	<i>unkn</i>		2	2	2
	Pyralidae	<i>Crambus</i>	Herbivore	3	3	3	
Coleoptera	unkn	<i>unkn</i>		5	5	3	
	Dytiscidae	<i>unkn</i>	Predator	51	1	1	
		<i>Agabus</i>	Predator		22	9	
		<i>Agabinus</i>	Predator		27	9	
		<i>Liodessus</i>	Predator		1	1	
	Elmidae	<i>unkn</i>		47	1	1	
		<i>Zaitzevia</i>	Scraper		1	1	
		<i>Optioservus</i>	Scraper		45	3	

ORDER	FAMILY	GENUS	Feeding Guild	Family total	Total	# of sites
	Tenebrionidae			3	3	3
	Staphylinidae		Predator	1	1	1
	Helophoridae	<i>Helophorus</i>	Herbivore	1	1	1
	Hydrophilidae	<i>Tropisternus</i>	Predator	1	1	1
	Haliplidae		Herbivore	1	1	1
	Scirtidae	<i>Cyphon</i>	Scraper	1	1	1
Odonata	Gomphidae		Predator	1	1	1
	Corduliidae	<i>Epithea</i>	Predator	6	6	1
	Libellulidae	<i>Sympetrum</i>	Predator	2	1	1
		<i>Macrothemis</i>	Predator		1	1
	Lestidae	<i>Lestes</i>	Predator	2	2	1
Diptera	unkn	<i>unkn</i>		8	8	5
	Chironomidae			11645	11645	30
	Tabanidae	<i>Chrysops</i>	Predator	7	5	4
		<i>unkn</i>	Predator		2	2
			Filter feeder			
	Culicidae		feeder	1	1	1
	Ceratopogonidae	<i>unkn</i>		61	5	2
		<i>Bezzia</i>	Predator		49	11
		<i>Dasyhelea</i>	Gatherers		5	2
		<i>Culicoides</i>	Predator		2	2
	Tipulidae	<i>unkn</i>		38	5	2
		<i>Dicranota</i>	Predator		31	11
		<i>Gonomyodes</i>			1	1
		<i>Molophilus</i>			1	1
	Simuliidae		Filter feeder	2131	2131	29
	Empididae	<i>unkn</i>	Predator	32	6	3
		<i>Chelifera</i>	Predator		11	7
		<i>Clinocera</i>	Predator		15	3
	Chaoboridae		Predator	1	1	1
	Ephydriidae	<i>Notiphila</i>	Gatherers	1	1	1
	Dolichopodidae		Predator	1	1	1
	Thaumaleidae	<i>Thaumalea</i>	Scraper	1	1	1
Hydra			Predator	41	41	6
Hirudinea			Predator		1	1
Gastropoda			Scraper	49	49	17
			Filter feeder			
Pelecypoda			feeder	253	253	17
Hydrachnida			Predator	511	511	29
Nematoda			Gatherers	517	517	29
Oligochaeta			Gatherers	1464	1464	30
Total					18435	

APPENDIX II Summary of all CCA and RDA ordinations

(A) Taxonomic Data in reference sites

Invert Data	Spatial Scale	Sites	Variance explained (%)		Strongest variables	Axis correlations		Randomization tests	
			all axes	axes 1&2		1	2	all axes	first axis
Taxa (CCA)	Local	all	51.6	25.5	finesub	0.5965	-0.299	0.002	0.058
					velocity	0.2821	0.5379		
					Canopy C	-0.462	-0.0746		
					lg10st_w	-0.3776	-0.3511		
	small rca	77.6	38	lg10Chla	0.6498	0.0353	0.09	0.258	
				velocity	0.437	-0.2154			
				lg10strm	-0.0463	0.3665			
	large rca	87.6	45.2	lg10strm	0.6918	-0.0486	0.024	0.11	
				.finesub	-0.6672	0.3906			
				Canopy C	0.5983	-0.02			
				total wo	-0.5574	0.1724			
	Riparian	all	40.3	21	CV_elev	0.1985	0.7516	0.146	0.568
					prophard	-0.6404	0.3655		
					lg10Rip_rca	0.4686	0.1413		
					rca	0.4478	0.2168		
small rca		53.3	31.1	tree Den	0.8233	0.1345	0.09	0.25	
				rcaBedr	0.1126	-0.6836			
				rcaCV_el	-0.0705	-0.3963			
large rca		58.7	37.8	prophard	0.9109	-0.1176	0.07	0.132	
				rcaCV_el	0.5524	0.4957			
Catchment		all	43.9	23.9	.Lake	0.41	0.4774	0.036	0.026
					.Wetland	-0.1689	0.4798		
					Strm_Lng	-0.527	-0.1166		
	small rca	52.6	33.4	CV_elev_	0.2268	0.8975	0.116	0.168	
				.Wetland	-0.2015	-0.6801			
				Eshd_sqm	0.645	-0.369			
	large rca	50.2	36.9	Eshd_sqm	-0.256	-0.9036	0.038	0.012	
				.Lake	0.7929	-0.4069			
				.Bedrock	-0.2683	-0.6351			

(B) Feeding guild data in reference sites

Invert Data	Spatial Scale	Sites	Variance explained (%)		Strongest variables	Axis correlations		Randomization tests		
			all axes	axes 1&2		1	2	all axes	first axis	
Feeding Guild (RDA)	Local	all	59.1	51.4	finesub	-0.1969	-0.4729	0.048	0.118	
					DO(mg/L)	-0.3928	0.3408			
					velocity	0.0589	0.3819			
		small rca	87.4	79.3	.finesub	-0.0145	-0.5783	0.098	0.072	
				total wo	-0.0659	-0.5588				
				Temp (°C)	0.4622	-0.0229				
		large rca	92.7	84.5	Canopy C	-0.562	-0.6612	0.078	0.022	
				lg10strm	0.1843	-0.6403				
				.finesub	-0.5781	0.5528				
		Riparian	all	37.5	31.7	CV_elev	-0.2774	0.392	0.452	0.414
					tree Den	0.3469	0.3836			
					rca10har	-0.1306	-0.3043			
			small rca	63.7	59.7	tree Den	0.7578	-0.1742	0.306	0.3
					lg10Rip_	-0.1768	-0.3726			
					rcaCV_el	-0.3048	-0.2567			
		large rca	47.3	42.5	rcaCV_el	0.7284	-0.1669	0.536	0.802	
				tree Den	0.5534	-0.0591				
				rca10har	-0.4329	-0.3312				
	Catchment	all	43.5	39.8	.Wetland	0.5937	-0.084	0.204	0.198	
					Eshd_sqm	-0.1173	-0.4839			
					CV_elev_	-0.4695	0.3201			
		small rca	85.4	80.4	.Bedrock	-0.3029	-0.6032	0.016	0.032	
				.Wetland	0.568	0.451				
				.Harv10	0.2223	0.4806				
		large rca	49.3	44.8	CV_elev_	-0.7804	-0.127	0.462	0.45	
				.Wetland	0.5757	-0.2419				
				.Bedrock	0.3881	0.1973				

(C) Taxonomic and feeding guild data and combined spatial scales

Invert Data	Spatial Scale	Sites	Variance explained (%)		R/C	Strongest variables	Axis correlations		Randomization tests	
			all axes	axes 1&2			1	2	all axes	first axis
Taxa (CCA)	Riparian and catchment	small rca	84.8	39.2	R	rcaBedr	0.0283	-0.6548	0.18	0.464
					R	tree Den	-0.6458	-0.0001		
					C	Eshd_sqm	0.6359	-0.1794		
					C	CV_elev_	0.1089	0.5537		
					C	.Harv10	0.4151	0.1708		
	riparian and catchment	large rca	82.6	45.3	R	prophard	0.8556	-0.2367	0.31	0.046
					C	.Lake	0.7442	0.2694		
					C	CV_elev_	0.5945	0.0331		
					R	lg10Rip_	-0.1607	0.588		
					R	tree Den	0.439	-0.2492		
Feeding guild (RDA)	riparian and catchment	small rca	92.8	83.1	R	tree Den	0.7376	-0.3716	0.142	0.302
					C	.Bedrock	-0.3086	-0.584		
					C	.Harv10	0.2277	0.4617		
					C	Eshd_sqm	-0.408	0.2489		
					R	rcaCV_el	-0.3127	-0.1719		
	riparian and catchment	large rca	53.7	47.2	R	rcaCV_el	-0.7278	-0.1297	0.888	0.74
					C	.Wetland	0.5887	-0.2164		
					R	tree Den	-0.5522	-0.0222		
					R	rcaBedr	0.4094	0.2446		
					C	.Harv10	-0.2182	0.2993		

APPENDIX III Stem densities of tree species

Densities of stems for each species in all sites in upland forest transects in trees/hectare estimated by point-center-quarter method

Site	RCA	Total Density	<i>Betula papyrifera</i>	<i>Picea mariana</i>	<i>Picea glauca</i>	<i>Abies balsamea</i>	<i>Pinus banksiana</i>	<i>Acer spicatum</i>	<i>Populus tremuloides</i>
RL2	Large	13331	200	400	333	2999	0	8065	0
RL3	Small	2400	200	0	0	200	0	1000	0
RL4	Large	7960	182	0	0	2473	0	2371	2934
RL5	Small	4600	400	400	0	3800	0	0	0
RL6	Small	5600	600	3200	0	1600	0	200	0
RL7	Small	3400	1400	0	200	800	0	1000	0
RL8	Large	4201	630	142	346	1730	0	519	0
RL9	Small	5200	1200	0	800	800	0	2400	0
RL10	Large	6461	1641	1186	0	3248	0	193	97
RL16	Large	4094	1382	1049	26	1638	0	0	0
RL23	Small	6000	600	2200	0	3200	0	0	0
RL24	Large	4804	260	1920	0	1811	692	0	120
RL25	Large	3667	1136	90	93	2020	0	327	0
RL26	Small	3600	1200	200	200	1600	0	400	0
RL27	Small	4800	1000	200	200	1200	0	2200	0
RL28	Small	5400	2800	200	200	1200	0	600	200
RL30	Small	11600	2800	5600	0	3200	0	0	0
RL31	Large	3057	168	1080	0	968	0	0	841
RL33	Small	7000	0	3400	0	0	3600	0	0
RL36	Small	6000	1600	2400	0	1800	0	0	0
RL39	Large	1071	0	948	12	12	87	0	0
RL45	Large	1212	0	1172	0	30	0	0	0
RL50	Large	3471	613	0	64	286	0	2308	200
RL1C	Large	1007	412	212	0	50	0	0	0
RL2C	Large	972	583	51	24	146	0	121	0
RL12C	Large	2298	698	1120	193	254	0	0	0
RL13C	Small	8200	2000	3800	200	2200	0	0	0
RL17C	Large	1416	12	1085	0	225	0	0	0
RL18C	Small	4800	2000	1800	0	1000	0	0	0
RL19C	Small	5200	800	600	0	3800	0	0	0

APPENDIX IV – Site list

List of sites used in study with site grouping information, and UTM coordinates using NAD 83 datum. Coordinates are all located in UTM grid 16.

Site ID	RCA	Harvested	Northing	Easting
2	Large	No	5433844	427409
3	Small	No	5430878	426243
4	Large	No	5422465	430465
5	Small	No	5425473	432049
6	Small	No	5425189	431871
7	Small	No	5438908	433722
8	Large	No	5426215	431814
9	Small	No	5426290	431950
10	Large	No	5435578	429645
16	Large	No	5437111	439491
23	Small	No	5446681	457604
24	Large	No	5454675	456436
25	Large	No	5417605	451095
26	Small	No	5417671	451257
27	Small	No	5422907	451109
28	Small	No	5421377	451095
30	Small	No	5452250	449170
31	Large	No	5455215	448039
33	Small	No	5453100	447542
36	Small	No	5452770	450407
39	Large	No	5451878	437286
45	Large	No	5454879	445371
50	Large	No	5417305	450465
1C	Large	Yes	5457859	424869
2C	Large	Yes	5458296	422705
12C	Large	Yes	5433889	440122
13C	Small	Yes	5433909	440284
17C	Large	Yes	5447394	454984
18C	Small	Yes	5447783	455164
19C	Small	Yes	5446891	455510