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Comparison of macroinvertebrate assemblages inhabiting pristine streams in the Huron Mountains of Michigan, USA

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Abstract

Benthic macroinvertebrate assemblages were surveyed from similar erosional biotopes of four pristine streams in the remote Huron Mountain region of the upper peninsula of Michigan during the summers of 1992 and 1993. Semi-quantitative samples from five sites, each in a 1.5 km stretch of Mountain Stream, Pine River, Salmon-Trout River and Huron River, were the basis for structural and functional comparisons between streams. Ancillary water chemistry data reflect the relative pollution free nature of these streams. Both water chemistry and macroinvertebrate data served as the first baseline data for Huron Mountain streams. No new or rare species were found among the 194 species sampled. Temporal differences in taxonomic makeup within streams were due to differences among insect species life cycles. Taxonomic makeup between streams was generally similar, but certain differences are shown to be possibly related to factors such as lake sources, interspecific interactions, and stream size. Based on relative abundance of each functional feeding group, assemblages in all streams were functionally similar and collector-dominated. ANOVA results indicated significant differences in functional feeding group abundance and biomass between streams in every case. The functional variations reflected by specific differences in taxonomic composition between stream assemblages are discussed.

Introduction

The general degradation of riverine habitats is an ever-increasing worldwide problem (Benke, 1990; Allan & Flecker, 1993) limiting our ability to understand the ecology of streams in their natural state. Despite recent efforts to curb pollution and restore damaged running water habitats, truly unaltered streams remain extremely scarce. The Huron Mountain region of the upper peninsula of Michigan is a somewhat remote area with low human population density. It is relatively protected from perturbations and is essentially pollution free. Access to this region provided us with an excellent and rare opportunity to study macroinvertebrates in truly pristine streams of a mid-temperate region of eastern North America.

Ecological surveys of benthic macroinvertebrates have been completed in neighboring areas, but most efforts have been confined to single streams (e.g., Hilsenhoff, 1972; Lillie & Hilsenhoff, 1992). Pennak (1977) argued that, instead of concentrating on the properties of individual streams, researchers might gain better ecological information by comparing streams within a region. Such an approach could be expected to generate reliable conclusions about the environmental processes that influence invertebrate communities on a regional scale (Hawkins et al., 1982; Malmqvist & Brönmark, 1984). In addition to confinement to single streams, most stream surveys, while providing some valuable distribution and abundance data on populations, have not provided the kind of broad scale ecological information that could serve as baselines for future measurements of community or ecosystem-level changes.

Our approach in this study was to inventory the macroinvertebrate fauna of a single productive biotope in each of four unpolluted streams in a small, relatively homogeneous study region using a structured sampling regime. By concentrating our efforts on one biotope, we were able to compare the structure and function of benthic macroinvertebrate assemblages between the streams. To strengthen the comparison, some abiotic parameters known to influence the distribution of macroinvertebrates in streams, including substrate size and heterogeneity (e.g., Cummins & Lauff, 1969), current velocity (e.g., Minshall & Minshall, 1977), and relative canopy cover (e.g., Hawkins et al., 1982) were standardized among all sample sites and streams as much as possible. No other comprehensive aquatic macroinvertebrate studies have been published for the Huron Mountain region. Thus, besides providing comparative data of heuristic value, the data herein can function as a practical baseline against which potential impacts of local increases in recreational or other land use in the Huron Mountains may be measured. Data on benthic species assemblages are particularly well suited for long term evaluation of stream conditions (see Rosenberg & Resh, 1993).

Methods

Study region

The Huron Mountain region of Michigan is a 233 km^2 area in northern Marquette and Baraga Counties on the south shore of Lake Superior (Figure 1). A private conservation-oriented organization, the Huron Mountain Club, owns and manages ca. 70 km^2 in the eastern portion of the region. This area is perhaps the most well-preserved remnant of old-growth northern hemlock-hardwood forest in the Great Lakes region (Flader, 1983).

Low mountains and rolling topography reflect the geology and glacial history of the region. The interior bedrock of this area consists primarily of Laurentian granite associated with the Canadian Shield, whereas Jacobsville sandstone forms the bedrock of the Lake Superior plain. Soils of this region are categorized as Munising loamy sand associations, products of weathered glacial till with moderate to rapid permeability (Berndt, 1988).

Located between 46 ° and 47 ° north latitude, the Huron Mountain region is subject to a boreal climate with normal monthly temperatures varying seasonally between 21 °C and −12 °C. The mean annual temperature is 6 °C, but extremes of 40 °C and −29 °C have been recorded. An average of 783 mm of precipitation falls on the area each year, most of it as snow.

Study streams

Benthic macroinvertebrate communities were sampled in Mountain Stream, Pine River, Salmon-Trout River, and Huron River, all part of the same drainage basin (Figure 2). We selected these streams because they represent typical lotic systems of the region and they contain physically similar erosional habitats. All of the study streams have glacially worked substrates, ranging from razor-sharp boulders and bedrock outcrops to rounded cobble, gravel, and coarse sands. All study streams are bordered by similar riparian vegetation consisting mainly of hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), red and white pine (*Pinus resinosa* and *P. strobus*, respectively), and deciduous hardwoods such as red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*).

Mountain Stream and Pine River are lake-connector streams that drain surface waters from Mountain Lake and Pine Lake, respectively. Although they are very short (respective lengths = 2.3 and 3.5 stream km) with relatively small watersheds (approximately 12 and 25 km^2, respectively), these streams have many characteristics of larger systems, including heterogeneous substrate, substantial discharge, and wide channels. Both are located entirely within the boundaries of the Huron Mountain Club and have no significant disturbances at any point along their banks.

The most distant headwaters of the Salmon-Trout River (38 stream km from its mouth) drain marsh-type wetlands on the Yellow Dog Plains in the Escanaba River and Michagamme State Forests. Ponds, bogs, springs, and runoff supply other first-order tributaries of this system. Most of the ca. 100 km^2 catchment is forested, however, some small areas of unwooded land in the upper reaches of this river may be remnants of clear-cuts from pulpwood harvesting.

The Huron River, at nearly 50 stream km in length and with a watershed area of approximately 200 km^2, is the largest stream in the study region. Its most distant tributary is fed by Charles Lake, but all other tributaries are fed by springs, wetlands, and runoff. Some small structures (mostly fishing, hunting, and logging camps) are scattered along the main course of the river and its tributaries, but no industries are present. A large paper company currently manages much of the Huron River catchment for production of Jack Pine (*Pinus banksiana*) monocultures. Red Pine (*Pinus resinosa*) is also selectively harvested from mature forests of the watershed. Although minimal, Huron River is subject

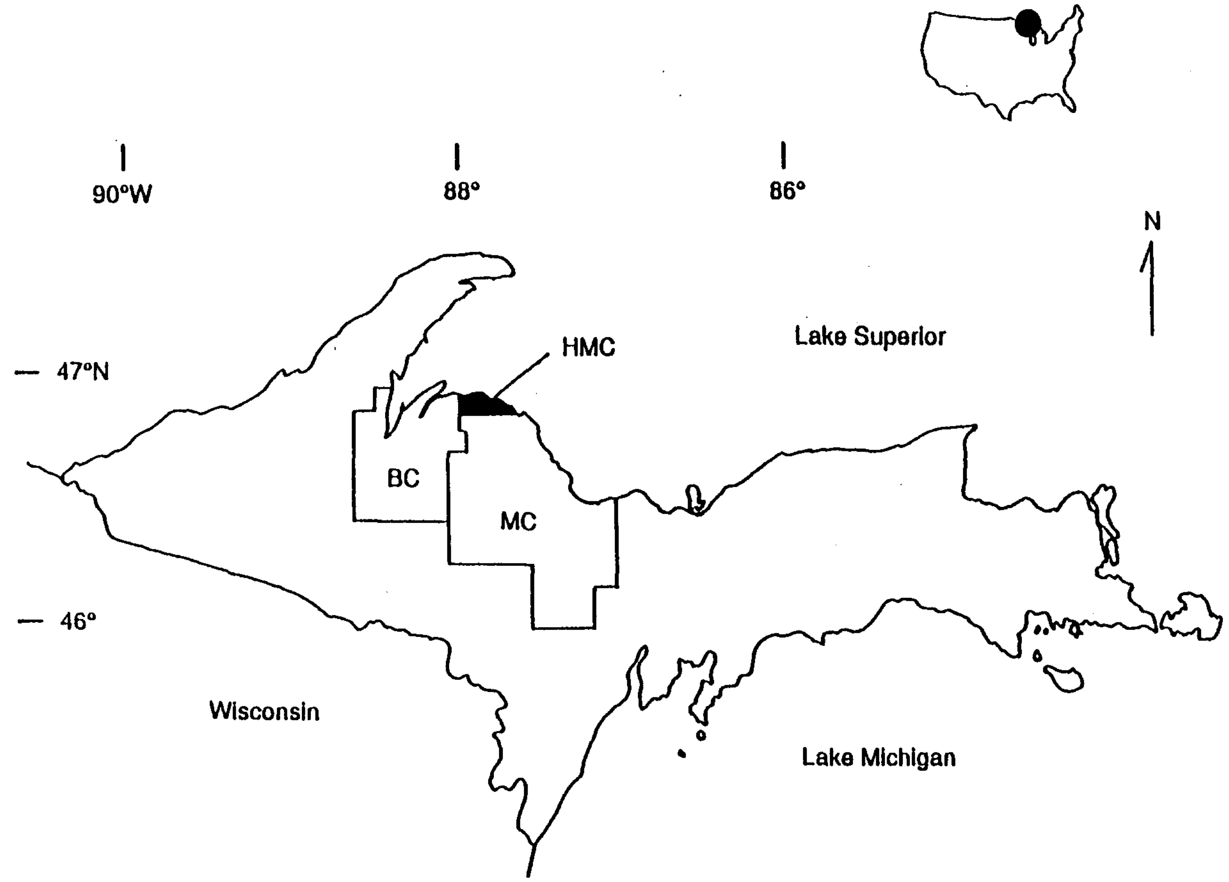

Figure 1. Map of the Michigan Upper Peninsula showing the general location of the Huron Mountain region. HMC = Huron Mountain Club, MC = Marquette County, BC = Baraga County. Scale: 1 cm ≈ 20 km

to the most anthropogenic disturbance relative to the other study streams.

Sampling areas and sites

In mid-June 1992, a small (1.5 km or less) segment of each stream containing five or more erosional zones was selected as the 'study area' of that stream. Study areas were chosen to ensure that they were abiotically similar between streams. Due to limited availability of erosional habitats on Pine River, the study area on that stream included only the first ca 500 m downstream from Pine Lake. Suitable habitats existed over the entire length of Mountain Stream, except for the first 300 m below Mountain Lake, which consisted primarily of exposed bedrock, and so was not included in the study area. Study areas on the Salmon-Trout and Huron Rivers were located in the middle to lower reaches where suitable sampling sites were abundant: 11 km upstream from the mouth of Huron River, and 15 km upstream from the mouth of Salmon-Trout River (Figure 2). Physical attributes of the study areas are given in Table 1.

Five sampling sites, each a section of stream approximately 5 m long, were established within the study area of each stream. All sampling sites were characterized by fairly homogeneous gravel and cobble substrates consisting of a mixture of sandstone and granite. In addition, all sites were 10–20 m wide, 0.10–0.25 m in mean depth, 10–50% shaded by riparian vegetation, and had current velocities ranging between 0.4 and 0.9 m s^{-1}. Similarities of substrate, depth, and flow velocity were given priority during site selection. Sampling sites were dispersed as much as possible within the study area of each stream, while still maintaining consistency of the biotope characteristics within and between streams.

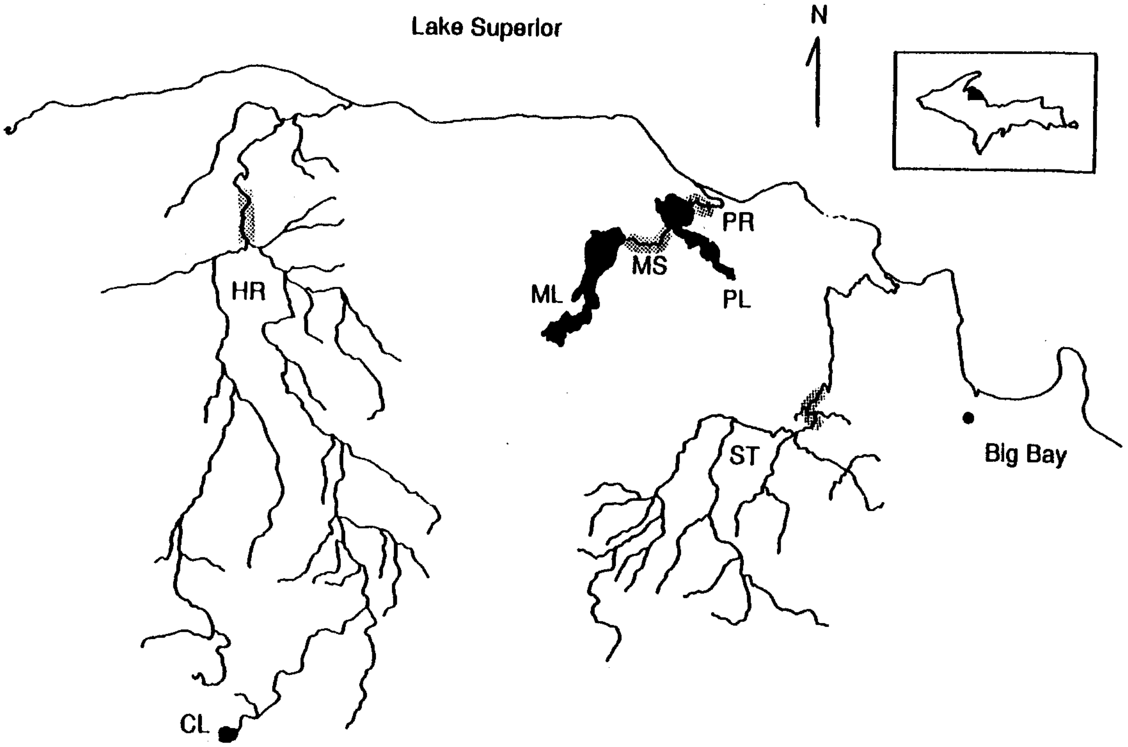

Figure 2. Map of the Huron Mountain region showing the location of study streams and sampling areas. CL = Charles Lake, HR = Huron River, ML = Mountain Lake, MS = Mountain Stream, PL = Pine Lakes, PR = Pine River, ST = Salmon-Trout River. Sampling areas are stippled. Scale: 1 cm ≈ 1.5 km

Sampling schedule

Sampling was conducted in middle and late summer (July and September) 1992 and early summer (May) 1993. Additional qualitative samples were taken in June 1992 and August 1993. A year-round study was prohibited by the inaccessibility of the region during periods of deep snow from late fall to early spring. The sampling periods, however, ensured that nearly all resident macrobenthos were present in postembryonic growth stages on at least one of the sampling dates. All samples from each stream were taken on the same day, and all streams were sampled within, at most, four days during each of the three sampling periods. This sampling protocol reduced the probability of overlooking benthic insect species with short emergence windows.

Biotic sampling

Benthic macroinvertebrates were semi-quantitatively collected with a surber sampler (0.09 m^2, 0.5 mm mesh) to a depth of ca. 10 cm from the five sampling sites on each study stream. Five surber samples were taken at each sampling site on each sampling date. Semi-quantitative kick samples (0.09 m^2, 0.5 mm mesh, ca. 10 cm depth) replaced surber samples during the early summer sampling period due to deep water conditions at some sites. Qualitative kick samples were taken from each sampling site on each sampling date and during the June 1992 survey to obtain voucher specimens for deposit in the Purdue University Entomological Research Collection (PERC). Emphasis was placed on collecting from the upstream portion of each riffle because this is where the greatest density of individuals can be expected (see e.g., Godbout & Hynes, 1982; Brown & Brown, 1984). In all, 300 semi-quantitative samples (5 samples per site × 5 sites per stream × 4 streams × 3 sampling dates) were taken.

All macroinvertebrates collected were immediately transferred to plastic bags and fixed in 90% ethanol. Macroinvertebrates were hand-picked from each semi-quantitative sample, identified, enumerated, and sorted into functional feeding groups (FFG's) after Cummins & Klug (1979). The organisms in each FFG were incubated at 50 °C until dry (usually 2–4 d) and weighed to the nearest 0.1 mg on a Mettler^{TM} AE-100 electron-

Table 1. Physical characteristics of study areas based 1992 field surveys. MS = Mountain Stream, PR = Pine River, ST = Salmon-Trout River, HR = Huron River.

	MS	PR	ST	HR
Order[a]	n/a	n/a	4	5
Gradient (%)	2.0	1.3	1.0	1.0
Coordinates				
Latitude	46°52'10"	46°53'02"	46°49'08"	46°52'10"
Longitude	87°53'10"	87°52'10"	87°48'28"	87°59'08"
Mean Depth (m)	0.15	0.15	0.16	0.15
Mean Width (m)	10.2	11.2	12.6	13.0
Substrate				
Type[b]	−6	−6	−6	−6
QD[c]	1	1	1	1.5
Canopy Cover (%)	33	10	25	10
Temperature (°C)[d]				
Mean	17.7	19.1	14.6	16.8
Range	9–24	11–23	9–20	11–22
Discharge (m^3 s^{-3})				
Mean	1.3	1.0	1.4	2.8
Range	1.0–1.9	0.6–1.8	0.9–1.8	1.2–4.6

[a] According to Strahler (1957), from 1:24,000 scale topographic maps, n/a = not applicable (see Hughes and Omernik 1981)

[b] Phi value of 50th percentile on a cumulative curve by weight

[c] Quartile deviation (Heterogeneity)

[d] Includes May 1993 data

ic balance. Dry macroinvertebrates were ignited in a Thermolyne™ 6000 muffle furnace at 550 °C for 4–6 h (depending on sample size) and ash-free dry weights (AFDW) calculated to 0.1 mg (see Brower et al., 1990).

Permanent macroinvertebrate collections from qualitative samples were transferred to 70% ethanol. Chironomids and minute specimens were cleared in 10% KOH or 85% lactic acid, dehydrated in ethanol and 2-ethoxyethanol (Cellosolve™), and slide mounted in balsam. Collected benthos were identified to the lowest taxonomic level possible based on available literature. Regional keys such as Ross (1944), Burks (1953), and Hilsenhoff (1981) were used for initial sorting and identification, with more specialized keys and taxonomic descriptions used as necessary. Some taxa (e.g., planaria and leeches) could not be identified after preservation in alcohol. When possible, living or narcotized (see Klemm, 1985) specimens of these taxa were used for identifications. Generic- and species-level identifications of Ephemeroptera, Plecoptera, Trichoptera, Acarina, and Chironomidae were verified by taxonomic specialists.

Abiotic sampling

A substrate sample was collected in June 1992 from each of the 20 sample sites to a depth of 15 cm using a metal cylinder (approx. diam. 16 cm). The collected particles were sorted by mean diameter according to the Wentworth scale (Wentworth, 1922) as modified by Cummins (1962). The typical substrate size recorded for each site equaled the Phi value of the 50th percentile on a cumulative curve by weight (Inman, 1952; Cummins, 1962; Minshall, 1984). Substrate heterogeneity was determined by quartile deviation, where QD = (Phi value of 25th percentile − Phi value of 75th percentile)/2 (DeMarch, 1976; Lamberti & Resh, 1979; Erman & Erman, 1984; Minshall, 1984). Canopy cover was visually estimated during June, 1992. Current velocity was measured at three points across each site with a Weathermeasure™ F583 pygmy current meter. This along with width and mean depth were determined at all sites on all sample dates.

One 500 ml water sample was collected from the study area of each stream in June, July, and September, 1992, and May and August, 1993, and transported to the laboratory for chemical analysis. The pH was determined to the nearest 0.1 unit in the field with Whatman™ color comparator strips and checked in the laboratory with an Orion Research™ #81 pH/millivolt meter. Conductivity was measured to the nearest 0.1 μS cm^{-1} with a Hanna™ HI-8033 conductivity meter, and ion analyses were performed with Dionex™ equipment. Phenolphthalein and total (bicarbonate) alkalinity were measured in the field with a LaMotte™ titration kit. Water temperature was measured several times on each sampling date.

Quantitative analyses

ANOVA's and Student-Newman-Keuls multiple comparison tests were used to identify differences in density (mean abundance and biomass per m^2) within each FFG between streams. Data were log transformed to correct for variance heterogeneity (Sokal & Rohlf, 1981). Statistical significance was based on $\alpha = 0.05$ and all statistical tests employed SAS procedures appropriate for a balanced design (SAS, 1989; Montgomery, 1991). For this study, temporal differences were not quantitatively analyzed, and data from different sample dates were pooled to reveal fundamental differences between the stream assemblages.

Results

Means and ranges of recorded stream temperatures and discharges are given in Table 1, and water chemistry data are summarized in Table 2. Phenolphthalein alkalinity was 0 in all field tests. Nitrate (NO_3^-), Nitrite (NO_2^-), and orthophosphate (PO_4^{3-}) occurred only in trace amounts (i.e., $\ll 0.05$ ppm) and were not detected in most samples. The study streams were virtually free of pollutants and no extreme differences in water chemistry existed between them.

The 194 different taxa (most identified to species) collected in this study and their percentage distribution within study streams and sampling periods are presented in Table 3. Note that the data are relative values and should be compared within columns only. Chironomid midges were the most abundant organisms in each sample, but several other taxa (e.g., the mayfly *Ephemerella dorothea* and the black fly *Prosimulium fuscum*) were very abundant on certain sample dates. All of the assemblages had similar taxonomic composition, although some species appeared to be limited in their distribution among streams.

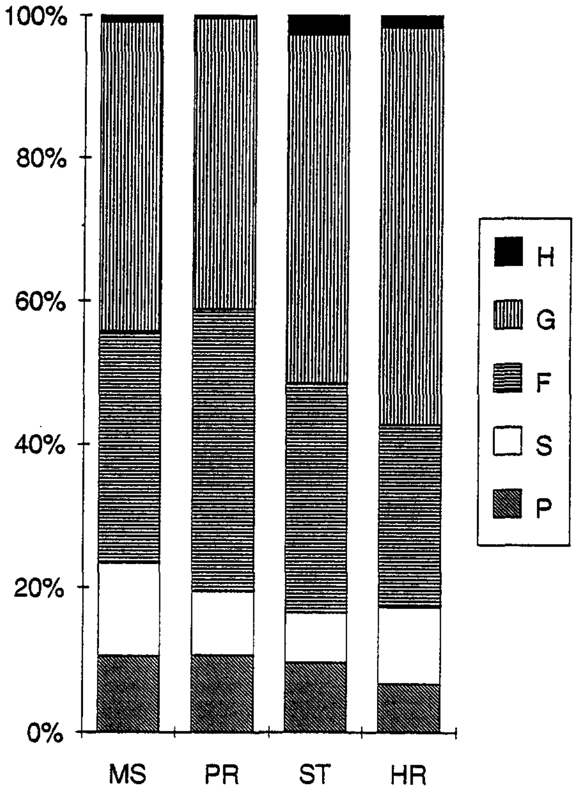

Figure 3. Trophic structure of study streams based on the total collection for each FFG. H = Shredders, G = Collector-gatherers, F = Collector-filterers, S = Scrapers, and P = Predators. MS = Mountain Stream, PR = Pine River, ST = Salmon-Trout River, HR = Huron River.

Trophic structure of assemblages in all of the study streams was similar, with collectors as the numerically dominant guild and shredders scarcely represented (Figure 3). ANOVA tests indicated that the mean abundance and biomass of organisms in each FFG differed significantly between study streams (Table 4). Pine River had the highest biomass, but lowest abundance, of shredders. Collector-gatherer abundance was relatively similar among streams, whereas collector-gatherer biomass was significantly higher in Salmon-Trout River. Mean collector-filterer biomass in Pine River exceeded that of the other streams by an order of magnitude. All streams had similar scraper biomass, but scraper abundance was greatest in Mountain Stream. Predator biomass and abundance were significantly lower in Huron River than any other streams.

Table 2. Means and ranges of water chemistry parameters taken at study areas, all sampling periods combined. MS = Mountain Stream, PR = Pine River, ST= Salmon-Trout River, HR = Huron River.

Stream	pH	Conductivity	Alkalinity	Na^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}
MS	7.6	107	53	2.2	1.5	3.5	14.6	1.1	4.3
	(7.4–7.8)	(90–127)	(46–60)	(1.0–4.0)	(0.8–2.5)	(2.1–5.2)	(11.7–16.3)	(0.5–1.4)	(3.4–6.6)
PR	7.2	99	45	1.6	0.9	2.3	12.3	1.0	5.0
	(6.7–7.6)	(82–114)	(42–50)	(1.0–2.3)	(0.8–1.2)	(1.7–2.7)	(9.7–14.5)	(0.5–1.4)	(3.6–8.4)
ST	7.7	127	63	1.9	1.3	3.8	17.9	1.1	3.0
	(7.4–7.8)	(101–147)	(50–78)	(1.1–3.0)	(0.9–2.0)	(3.5–4.2)	(16.7–19.8)	(0.4–2.0)	(3.1–3.6)
HR	7.6	93	40	1.4	0.8	2.4	10.9	1.5	3.2
	(7.2–7.8)	(56–122)	(28–60)	(1.1–1.8)	(0.7–1.0)	(2.1–2.8)	(9.4–12.5)	(0.3–2.9)	(2.4–4.6)

NOTE: Parenthetical values are ranges. Conductivity measured in $\mu S\ cm^{-1}$, alkalinity in $mg\ l^{-1}\ CaCO_3$, and all ions in $mg\ l^{-1}$.

Discussion

Assemblage structure

The streams of the Huron Mountain region support very diverse assemblages of benthic macroinvertebrates, of which we have documented only a small fraction. Despite the general lack of anthropogenic disturbance in the region and our intensive sampling regime, no new or exceptionally rare species were collected. Because no macrobenthic faunal lists have previously been published for Huron Mountain streams, our data provide a foundation for future comparisons.

Although new or rare species were not found, several species listed in Table 3 may appear anomalous because they generally have not been associated with mid-stream riffle habitats. The burrowing mayfly *Ephemera simulans*, the ceratopogonid midge *Serromyia* sp., and the dragonflies *Macromia illinoiensis* and *Neurocordulia yamaskanensis* are normally found in depositional areas, and the few individuals collected were evidently drifting during or just before sampling. Many of the chironomid midge species collected, especially *Microspectra* sp. and *Microtendipes pedellus*, are typically associated with lentic or slow lotic habitats. The abundance of these species in our samples suggests that riffles may be a possible but otherwise uncommon habitat for them.

The variation observed within streams (between sample dates) (Table 3) basically has a phenological basis and reflects differences in life history patterns between species. Larvae of some species, for example, the mayfly *Acentrella turbida*, the stonefly *Paracapnia angulata*, and the caddisfly *Dolophilodes distinctus*, were absent only from the early season samples, presumably because individuals were eggs or very early instar larvae during that period. Other species, for example, the mayfly *Ephemerella dorothea*, the caddisfly *Hydroptila* sp., and the black fly *Prosimulium fuscum*, were abundant in the early part of the season and absent from subsequent samples, primarily due to May–June adult emergence (cf. Merritt et al., 1978). The early emerging mayfly *Ephemerella subvaria* (c.f. Leonard & Leonard, 1962) and perlodid stoneflies (c.f. Hilsenhoff & Billmyer, 1973) were represented in early samples by some remaining mature larvae, but did not appear again (as early instar larvae) until the late sampling period. Similar patterns were observed for the crane fly *Antocha* sp. and the chironomid midges *Stempellina* sp. and *Lopescladius hyporheicus* in certain streams.

Between-stream variation in assemblage structure is difficult to explain given the descriptive scope of this study and the lack of autecological data for many species. The streams' contrasting sources of water, however, explain some differences in taxonomic composition. Organisms more commonly associated with lentic habitats, like *Spongilla lacustris* (Porifera), *Hydra* spp. (Coelenterata), and *Orconectes propinquus* (Decapoda), are often collected in associated lake drainages (Graenicher, 1913; Smith, 1921; Slobodkin & Bossert, 1991), as in lake-fed Mountain Stream and Pine River. In addition, lake drainage streams have unique nutrient and abiotic conditions (see review by Richardson & Mackay, 1991) to which certain species, possibly including the filter-feeding caddisfly *Chimarra aterrima*, may be especially well adapted. Moreover, relatively warm water is typical of epilimnetic lake drainages (Ulfstrand, 1968; Hynes, 1970). Although temperature was perhaps the most important abiotic difference between streams, with means slightly higher in Mountain Stream and Pine River (Table 1),

Table 3. Distribution of collected macroinvertebrates among study streams and sampling periods. MS = Mountain Stream, PR = Pine River, ST = Salmon-Trout River, HR = Huron River, E = Early summer, M = Middle summer, L = Late summer. Values are percent abundance per stream per sampling period. o = fewer than 5 individuals collected (≪ 0.5%), - = not present.

	MS			PR			ST			HR		
Taxon	E	M	L	E	M	L	E	M	L	E	M	L
PORIFERA												
Spongillidae												
Spongilla lacustris	-	o	o	-	o	o	-	-	-	-	-	-
COELENTERATA												
Hydridae												
Hydra sp	o	-	-	o	-	-	-	-	-	-	-	-
TURBELLARIA												
Planariidae												
Dugesia tigrina	<1	o	o	1	<1	<1	<1	o	-	o	o	<1
Phagocata sp.	-	-	-	-	-	-	<1	<1	<1	-	-	-
NEMATOMORPHA												
Gordiidae												
Gordius sp.	-	-	o	-	-	-	-	-	o	-	-	o
ANNELIDA												
LUMBRICULIDA												
Lumbriculidae												
Lumbriculus variegatus	<1	2	1	<1	1	1	<1	<1	1	o	1	o
HIRUDINEA												
Erpobdellidae												
Dina parva	-	-	-	-	-	-	-	-	-	o	o	o
Glossiphoniidae												
Placobdella sp.	-	-	-	-	-	-	-	-	<1	-	-	-
CRUSTACEA												
ISOPODA												
Asellidae												
Caecidotea racovitzai	-	-	-	-	-	-	-	o	-	-	-	-
Lirceus lineatus	-	-	-	o	-	-	-	-	-	-	-	-
AMPHIPODA												
Gammaridae												
Gammarus pseudolimnaeus	-	-	-	-	-	-	o	<1	o	-	-	o
Hyalellidae												
Hyalella azteca	-	-	-	o	o	o	-	-	-	-	-	-
DECAPODA												
Cambaridae												
Orconectes propinquus	o	o	o	o	o	o	-	-	-	-	-	-
ACARINA												
Aturidae												
Aturus estellae	-	-	-	-	-	-	-	-	o	-	-	-
Hydryphantidae												
Protzia sp.	-	-	-	-	-	-	-	-	o	-	-	-
Hygrobatidae												
Atractides sp.	-	-	-	-	-	-	-	o	<1	-	-	-
Hygrobates sp.	-	-	-	-	-	-	-	o	o	-	-	o
Lebertiidae												
Lebertia sp.	-	-	-	-	-	-	o	-	<1	-	-	<1
Sperchontidae												
Sperchon sp.	<1	o	<1	-	-	o	o	<1	<1	-	o	<1
Torrenticolidae												

Table 3. Continued

	MS			PR			ST			HR		
Taxon	E	M	L	E	M	L	E	M	L	E	M	L
Torrenticola sp.	-	-	o	-	-	o	-	-	-	-	-	-
INSECTA												
EPHEMEROPTERA												
Baetidae												
Acentrella turbida	-	o	<1	-	<1	1	-	1	1	-	6	2
Acerpenna pygmaea	-	-	-	o	<1	o	-	-	-	-	-	-
Baetis armillatus	-	-	-	-	-	-	-	o	-	-	-	-
Baetis brunneicolor	-	-	-	-	-	-	-	1	-	-	<1	-
Baetis flavistriga	-	<1	<1	-	2	3	-	12	<1	-	5	-
Baetis intercalaris	-	1	1	-	-	-	-	-	-	-	1	o
Baetis punctiventris	-	-	-	-	-	-	-	o	-	-	-	-
Baetis tricaudatus	4	1	<1	-	o	-	5	3	o	2	2	-
Baetis spp.	o	-	o	-	o	-	o	4	-	o	<1	-
Ephemerellidae												
Attenella margarita	-	-	1	-	-	-	-	-	-	-	-	-
Timpanoga simplex	-	-	-	-	-	-	-	<1	-	-	o	o
Drunella cornuta	-	-	-	-	-	-	<1	o	-	-	<1	-
Drunella cornutella	-	-	-	-	-	-	-	-	-	3	-	-
Ephemerella dorothea	1	-	-	4	-	-	31	-	-	3	-	-
Ephemerella subvaria	1	-	-	4	-	3	3	o	3	<1	-	4
Eurylophella bicolor	-	-	-	<1	-	-	-	-	-	-	-	-
Eurylophella versimilis	-	-	-	-	-	-	-	-	-	-	o	-
Serratella deficiens	-	<1	o	-	5	<1	-	-	-	-	<1	-
Serratella serratoides	<1	-	-	-	-	-	-	-	-	-	-	-
Ephemeridae												
Ephemera simulans	-	-	-	o	-	-	-	-	-	-	-	-
Heptageniidae												
Heptagenia pulla	-	-	-	-	-	-	-	-	<1	-	-	-
Epeorus vitreus	4	1	1	-	o	-	o	<1	o	o	-	2
Leucrocuta hebe	-	1	-	-	<1	-	-	<1	-	-	6	-
Rhithrogena impersonata	-	-	-	-	-	-	-	o	1	-	-	5
Rhithrogena pellucida	-	-	-	-	-	-	-	-	-	-	1	-
Rhithrogena undulata	-	-	-	-	-	-	<1	-	-	5	-	-
Stenacron interpunctatum	-	-	-	o	-	-	o	-	-	-	-	-
Stenonema modestum	-	<1	-	1	1	-	-	-	-	-	-	-
Stenonema pulchellum	-	-	-	-	o	-	-	-	-	-	-	-
Stenonema terminatum	-	-	-	-	-	-	-	-	-	-	o	1
Stenonema vicarium	1	-	3	o	-	2	-	<1	o	o	-	<1
Isonychiidae												
Isonychia bicolor	-	-	-	-	-	-	-	-	-	-	1	o
Leptophlebiidae												
Paraleptophlebia adoptiva	1	-	6	-	-	-	<1	-	-	<1	-	5
Paraleptophlebia guttata	-	1	-	-	-	-	-	o	-	-	-	-
Paraleptophlebia mollis	1	-	-	-	-	-	-	1	8	-	4	-
Paraleptophlebia volitans	-	-	-	o	o	<1	-	-	-	-	-	-
Leptohyphidae												
Tricorythodes minutus	-	-	-	-	o	-	-	-	-	-	<1	-
ODONATA												
Aeshnidae												
Boyeria vinosa	o	1	<1	<1	<1	<1	-	o	o	o	o	o

Table 3. Continued

	MS			PR			ST			HR		
Taxon	E	M	L	E	M	L	E	M	L	E	M	L
Calopterygidae												
Calopteryx maculata	-	-	-	-	-	-	-	-	o	-	o	o
Cordulegastridae												
Cordulegaster maculatus	-	-	o	o	-	-	-	o	o	o	o	o
Corduliidae												
Neurocordulia yamaskanensis	-	-	-	o	-	-	-	-	-	-	-	-
Gomphidae												
Hagenius brevistylus	-	-	-	o	-	-	-	-	-	-	-	-
Hylogomphus brevis	o	-	-	-	-	-	-	-	-	-	-	-
Ophiogomphus carolus	-	<1	<1	<1	<1	o	<1	<1	<1	o	<1	o
Stylogomphus albistylus	<1	<1	<1	1	<1	<1	-	-	-	-	-	-
Macromiidae												
Macromia illinoiensis	-	-	-	-	o	-	-	-	-	-	-	-
PLECOPTERA												
Capniidae												
Paracapnia angulata	-	o	1	-	-	-	-	o	1	-	o	<1
Chloroperlidae												
Alloperla sp.	o	-	o	o	-	-	o	o	o	<1	o	o
Haploperla brevis	<1	-	-	-	-	-	-	-	-	-	-	-
Leuctridae												
Leuctra tenella	-	o	o	-	-	-	-	o	-	-	1	-
Leuctra tenuis	-	1	-	-	o	-	-	-	-	-	<1	<1
Nemouridae												
Amphinemura linda	-	-	-	-	-	-	-	-	-	-	o	-
Prostoia completa	<1	-	-	o	-	-	-	-	-	-	-	-
Perlidae												
Acroneuria lycorias	1	1	1	2	1	1	-	o	o	1	<1	<1
Paragnetina media	<1	<1	<1	<1	1	1	-	<1	o	-	o	-
Perlodidae												
Isoperla cotta	-	-	-	o	-	-	<1	-	<1	-	-	-
Isoperla frisoni	-	-	-	1	-	-	-	-	-	<1	-	-
Isoperla lata	-	-	1	-	-	1	-	-	<1	-	-	<1
Isoperla richardsoni	-	-	-	o	-	-	-	-	-	-	-	-
Isoperla signata	-	-	-	-	-	1	1	o	1	<1	o	1
Isoperla transmarina	<1	-	-	-	-	-	o	-	-	-	-	-
Isogenoides doratus	-	-	-	-	-	-	-	-	-	o	o	<1
Isogenoides frontalis	-	-	-	-	-	-	o	-	o	o	-	-
Isogenoides olivaceus	-	-	-	-	-	-	-	-	1	-	-	<1
Isogenoides sp.	-	-	-	-	-	-	o	o	-	o	-	-
Pteronarcyidae												
Pteronarcys dorsata	-	-	-	-	-	-	<1	<1	<1	o	o	o
Taeniopterygidae												
Taeniopteryx burksi	o	-	-	-	-	-	o	-	<1	-	-	<1
MEGALOPTERA												
Corydalidae												
Corydalus cornutus	<1	<1	<1	<1	<1	<1	-	-	-	<1	<1	<1
TRICHOPTERA												
Brachycentridae												
Brachycentrus americanus	-	-	-	-	-	-	1	<1	1	-	-	-
Brachycentrus numerosus	-	-	-	-	-	-	<1	1	<1	o	1	<1

Table 3. Continued

Taxon	MS			PR			ST			HR		
	E	M	L	E	M	L	E	M	L	E	M	L
Glossosomatidae												
Glossosoma sp.	2	5	2	3	3	<1	-	-	<1	o	<1	<1
Protoptila sp.	-	-	-	-	-	-	2	-	-	-	-	-
Helicopsychidae												
Helicopsyche borealis	o	o	<1	2	1	1	-	-	o	1	2	1
Hydropsychidae												
Arctopsyche ladogensis	-	-	-	-	-	-	-	<1	o	-	<1	o
Ceratopsyche alhedra	-	-	-	-	-	-	-	-	1	-	-	-
Ceratopsyche bifida grp.	-	o	-	2	2	6	-	<1	<1	o	1	1
Ceratopsyche morosa	-	-	-	1	3	1	-	-	-	<1	-	1
Ceratopsyche slossonae	-	-	-	o	o	<1	<1	o	1	1	<1	1
Ceratopsyche sparna	<1	2	1	-	-	-	o	<1	<1	-	-	-
Ceratopsyche walkeri	-	-	-	<1	o	o	-	-	-	1	o	2
Cheumatopsyche sp.	-	<1	1	2	4	4	-	1	1	o	1	1
Hydropsyche betteni	-	-	-	-	<1	o	-	-	-	-	-	-
Hydroptilidae												
Hydroptila sp.	-	-	-	2	-	-	o	-	-	3	-	-
Leucotrichia pictipes	-	o	-	<1	<1	<1	-	-	o	-	-	-
Lepidostomatidae												
Lepidostoma sp.	o	o	-	o	-	-	1	<1	4	<1	o	2
Leptoceridae												
Ceraclea diluta	o	-	-	o	-	-	-	-	-	-	-	-
Ceraclea punctata	-	-	-	-	o	o	-	-	-	-	-	-
Oecetis inconspicua	-	-	-	o	-	-	-	-	-	-	-	-
Setodes sp.	-	-	-	o	-	-	-	-	-	-	-	-
Limnephilidae												
Goera stylata	-	-	-	-	-	-	<1	o	o	-	-	-
Neophylax nacatus	<1	-	-	1	-	-	<1	-	-	-	-	-
Pycnopsyche sp.	-	-	-	<1	-	-	-	-	-	o	o	-
Philopotamidae												
Chimarra aterrima	<1	1	3	<1	o	o	-	-	-	-	-	-
Chimarra obscura	-	-	-	2	<1	8	-	-	-	-	-	-
Dolophilodes distinctus	-	1	1	-	-	-	-	<1	1	-	2	2
Polycentropodidae												
Neureclipsis sp.	-	-	-	<1	o	1	-	-	-	-	-	-
Polycentropus sp.	-	-	-	-	-	-	-	-	-	-	<1	<1
Rhyacophilidae												
Rhyacophila fuscula	o	<1	<1	-	-	-	-	-	o	o	o	<1
COLEOPTERA												
Dryopidae												
Helichus lithophilus	-	-	-	-	-	-	-	-	-	o	-	o
Elmidae												
Dubirhaphia minima	-	-	-	o	-	-	-	-	-	-	-	-
Macronychus glabratus	o	-	-	o	-	-	-	-	-	-	-	-
Optioservus fastiditus	-	-	-	-	-	-	<1	1	o	o	6	o
Optioservus trivittatus	<1	6	4	o	1	2	1	1	1	2	1	1
Optioservus sp.	-	-	-	-	-	-	1	6	6	-	<1	5
Stenelmis crenata	2	6	3	3	4	1	-	o	-	-	-	-
Psephenidae												
Ectopria nervosa	-	-	-	-	o	-	-	-	-	-	-	-

Table 3. Continued

Taxon	MS			PR			ST			HR		
	E	M	L	E	M	L	E	M	L	E	M	L
DIPTERA												
Athericidae												
Atherix variegata	1	1	2	o	o	o	2	5	4	1	1	1
Blephariceridae												
Blepharicera tenuipes	o	-	-	-	-	-	-	-	-	-	-	-
Ceratopogonidae												
Probezzia sp.	<1	1	1	-	1	o	<1	1	<1	o	1	<1
Serromyia sp.	-	-	-	o	-	-	-	-	-	-	-	-
Chironomidae												
Chironominae												
Cryptochironomus sp.	-	-	-	o	<1	-	-	-	-	-	-	-
Demicryptochironomus sp.	-	-	-	o	-	-	-	o	-	-	-	-
Micropsectra sp.	-	-	-	-	-	-	-	<1	4	-	11	3
Microtendipes pedellus	<1	1	1	4	<1	1	<1	-	-	-	<1	1
Nilothauma sp.	-	-	-	-	-	-	-	-	-	-	-	o
Polypedilum aviceps	8	15	10	-	-	-	11	1	11	<1	1	-
Polypedilum convictum grp.	-	-	-	13	26	16	-	-	-	24	11	21
Polypedilum laetum	o	1	o	-	-	1	-	-	1	-	3	2
Rheotanytarsus spp.	5	18	12	13	8	5	21	48	20	23	16	17
Robackia cf. *demeijerei*	o	<1	<1	o	o	o	-	-	-	-	o	-
Stempellina sp.	4	<1	9	-	-	-	-	-	-	2	o	2
Diamesinae												
Diamesa sp.	o	1	<1	-	<1	<1	-	-	-	-	-	-
Potthastia longimana grp.	-	-	-	-	-	-	-	o	<1	<1	<1	<1
Orthocladiinae												
Chaetocladius sp.	-	-	-	1	<1	o	-	o	<1	-	<1	-
Corynoneura sp.	o	o	o	-	-	-	-	o	o	-	-	-
Cricotopus trifascia grp.	-	-	-	-	<1	5	<1	<1	3	3	1	<1
Cricotopus cf. *vierriensis*	o	-	-	-	-	-	-	-	-	-	-	-
Cricotopus/Orthocladius spp.	o	-	-	2	-	-	1	1	1	-	<1	-
Eukiefferiella claripennis grp.	-	-	-	-	<1	-	4	1	4	-	2	-
Eukiefferiella coerulescens	5	o	3	-	-	-	-	o	<1	-	-	-
Eukiefferiella devonica grp.	-	-	-	-	-	-	<1	<1	-	-	-	-
Eukiefferiella gracei grp.	-	-	-	<1	2	-	-	-	-	20	1	2
Georthocladius sp.	-	-	o	-	-	-	-	-	-	-	-	-
Lopescladius hyporheicus	<1	o	10	5	<1	10	-	-	-	-	2	-
Nanocladius rectinervis	<1	1	1	-	-	-	-	-	o	-	-	<1
Orthocladius carlatus	-	-	-	-	-	-	-	o	o	-	-	-
Rheocricotopus atripes grp.	7	o	-	-	-	-	o	o	-	-	-	-
Smittia sp.	o	-	-	-	-	-	-	-	-	-	-	-
Synorthocladius sp.	-	-	-	-	<1	-	<1	o	2	-	-	-
Thienemanniella sp.	o	o	<1	-	-	-	-	-	o	-	-	<1
Tvetenia discoloripes grp.	9	6	10	4	3	6	11	1	6	o	3	6
Tvetenia cf. *paucunca*	-	1	-	-	-	-	-	<1	1	-	-	-
Tanypodinae												
Conchapelopia sp.	-	3	1	3	7	o	-	-	-	-	<1	<1
Helopelopia sp.	-	3	-	-	<1	2	<1	<1	<1	<1	<1	-
Meropelopia americana	-	-	-	1	1	1	-	o	<1	-	-	-
Nilotanypus sp.	-	-	-	o	-	-	-	-	o	-	-	-
Rheopelopia sp.	1	1	1	1	1	-	<1	<1	3	<1	o	2

Table 3. Continued

	MS			PR			ST			HR		
Taxon	E	M	L	E	M	L	E	M	L	E	M	L
Thienemannimyia grp.	-	-	-	-	-	-	o	-	-	-	-	-
Empididae												
Chelifera sp.	-	-	-	-	-	-	-	o	o	-	-	-
Hemerodromia sp.	<1	1	<1	1	<1	<1	o	<1	o	o	o	o
Simuliidae												
Prosimulium fuscum	37	-	-	-	-	-	-	-	-	-	-	-
Simulium tuberosum grp.	-	<1	1	2	<1	-	<1	2	<1	2	1	o
Simulium venustum	o	-	-	-	-	-	-	-	-	<1	-	o
Simulium vittatum	-	-	-	<1	<1	1	-	-	-	-	-	-
Tipulidae												
Antocha sp.	1	-	<1	-	-	o	<1	-	<1	o	-	<1
Dicranota sp.	o	o	o	-	<1	-	-	o	<1	-	o	<1
Hexatoma sp. A	-	-	-	-	o	o	-	<1	<1	-	o	<1
Hexatoma sp. B	-	-	-	<1	o	<1	<1	1	<1	<1	1	o
Hexatoma sp. C	o	11	<1	1	1	1	-	-	<1	o	1	<1
Hexatoma sp. D	-	-	<1	o	<1	o	<1	1	-	<1	o	<1
Ormosia sp.	o	-	-	-	-	-	-	o	-	o	o	-
Pseudolimnophila sp.	-	-	o	-	-	-	-	-	-	o	-	-
Tipula abdominalis	-	o	-	o	-	o	-	<1	o	-	<1	o
Tipula caloptera	-	-	-	o	-	o	-	o	o	-	o	o
Tipula (Schummelia) sp.	-	-	-	o	-	-	-	-	-	-	-	-
MOLLUSCA												
GASTROPODA												
Ancylidae												
Ferrissia rivularis	-	-	-	-	-	-	-	-	o	-	o	<1
Lymnaeidae												
Fossaria humilis	-	-	-	<1	-	-	-	-	-	-	-	-
Physidae												
Physella sp.	-	-	-	<1	o	o	<1	o	<1	o	<1	<1
Planorbidae												
Gyraulus parvus	-	o	-	-	-	o	-	-	-	-	-	<1
Menetus sp.	-	-	-	-	-	-	-	-	-	-	-	o
PELECYPODA												
Sphaeriidae												
Sphaerium nitidum	1	3	4	12	17	12	o	o	o	o	-	-
Sphaerium rhomboideum	-	-	-	<1	<1	<1	-	-	-	-	-	-
Sphaerium simile	-	-	-	<1	o	o	-	-	-	-	-	-
Sphaerium sp.	-	-	-	o	<1	o	o	-	-	-	o	-

additional data, especially continuous long term measurements for all streams, are needed before thermal regimes can be effectively compared.

Our data suggest that interspecific interactions are important determinants of assemblage structure in the study streams. The conspicuous absence of the megalopteran *Corydalus cornutus* from Salmon-Trout River, for example, was balanced by greater abundances of other predators, specifically perlid stoneflies and the dipteran *Atherix variegata*, and may be indicative of competitive exclusion. Similarly, the filter-feeding caddisflies *Chimarra obscura* and *Neureclipsis* sp. seemed to take the place of *Dolophilodes distinctus* in Pine River. The near absence of the chironomid midge *Polypedilum aviceps* in assemblages containing an abundance of the *P. convictum* group may also

Table 4. Geometric means and ANOVA F-values for biomass and abundance within each FFG, all sample dates combined. $N = 300$ and df = 3,280 for each test. All data were log transformed for analyses. Within rows, means followed by the same letter are not significantly different. MS = Mountain Stream, PR = Pine River, ST = Salmon-Trout River, HR = Huron River.

Variable	MS	PR	ST	HR	F-Value
Biomass (AFDW mg m^{-2})					
Shredders	34.5 c	405 a	224 b	75.0 c	40.59*
Collector-Gatherers	91.1 b	103 b	230 a	116 b	10.66*
Collector-Filterers	75.1 b	518 a	63.6 b	44.4 b	39.92*
Scrapers	119 a,b	153 a	94.8 b,c	68.8 c	7.32*
Predators	485 a	383 a	375 a	136 b	19.47*
Abundance (Mean no. per m^2)					
Shredders	26 b	11 c	43 a	26 b	32.31*
Collector-Gatherers	1394 a	968 b	1248 a	1016 b	6.08*
Collector-Filterers	631 b	820 a	876 a	420 c	14.75*
Scrapers	439 a	208 b	162 c	156 c	36.35*
Predators	285 a	238 a	218 a	92 b	24.12*

* Significant for $\alpha = 0.05$

reflect competitive exclusion. Biotic factors other than interspecific interactions, including nutrient availability and behavioral adaptations, may explain some of the observed distributional patterns, but require additional investigation.

Distributions of some macroinvertebrate species have been associated with stream size (e.g., Brönmark et al., 1984; Strayer, 1990) and differences in study stream length and watershed area (see above) may contribute to between stream variation in assemblage structure. Stream size differences may explain the presence of the mayfly *Isonychia bicolor* in Huron River exclusive of the other study streams. The limited distribution of this species in the study region corroborates the results of Yanoviak & McCafferty (1995) which suggested that *I. bicolor* is most often found at stream sites 35–40 km from the source. Stream size and size-related factors (e.g., thermal regime) may also influence distributions of other species collected in this study.

Assemblage function

In terms of relative abundance of each FFG (Figure 3), the study streams are very similar and closely approximate the predictions of Vannote et al. (1980) for heterotrophic 3rd to 5th order systems. The functional similarity of the assemblages between streams reflects the consistency of the biotope sampled and the restricted geographic nature of this study. Nonetheless, some sections of the study streams are conspicuously different with respect to macrohabitat availability and diversity. For example, debris dams are less common on upper Pine River than the other streams, and much of the lower Huron River flows over exposed sandstone bedrock. Comprehensive surveys that include additional biotopes may therefore reveal more substantial functional differences between these streams.

The collection of many semi-quantitative samples exclusively from one biotope enabled us to compare both FFG abundance and FFG biomass between assemblages with satisfactory statistical power (Sokal & Rohlf, 1981). Several of the significant differences between streams (Table 4) are attributable to taxonomic differences between the sampled assemblages (Table 3) as discussed below.

The incongruous difference between shredder abundance (significantly lowest among streams) and biomass (significantly highest among streams) in Pine River is due to the presence of a patchily distributed and large-bodied facultative shredder, the crayfish *Orconectes propinquus*. Although *O. propinquus* was also present in Mountain Stream, fewer individuals were collected and the sample means were not so strongly influenced. The significant differences in shredder biomass and abundance between Salmon-Trout River and Huron River are primarily attributed to *Pteronarcys dorsata*, another large and patchily distributed shredder that was more common in Salmon-Trout River samples.

Large populations of chironomid midges were chiefly responsible for the numerical dominance of collector-gatherers in all of the assemblages. Because of their small body size, however, even great numbers of midges constituted only a minute fraction of the total biomass sampled. Other larger gatherers, including ephemerellid and leptophlebiid mayflies, were very common on some sample dates. The mayfly *Ephemerella dorothea*, for example, dominated the early summer samples from Salmon-Trout River (Table 3) and was the principal contributor to significantly higher collector-gatherer biomass in that stream.

Taxonomic differences are also responsible for the dramatic contrast in collector-filterer biomass between Pine River and the other streams. Species of large-bodied hydropsychid caddisflies and sphaeriid clams were the most common filter-feeding members of the Pine River assemblages, whereas minute *Rheotanytarsus* spp. midges were the primary filterers of the other streams. Proximity of sample sites to the source lake also influenced the Pine River filterer biomass. The standing crop of collector-filterers in lake drainages is often extremely high at the lake outlet and rapidly declines with distance from the lake (e.g., Sheldon & Oswood, 1977; Brönmark & Malmqvist, 1984). Although we did not recognize such a pattern during collection of Pine River samples, this phemonenon may have contributed to the observed difference in filterer biomass. Mountain Stream also receives surface water from a large lake, but samples were taken further downstream where lake effects become less pronounced.

Significantly high scraper abundance in Mountain Stream is due to the comparatively large number of elmid beetles collected there. Glossosomatid caddisflies were generally more common in Pine River and Mountain Stream, and contribute to the larger mean scraper biomass in those streams. Algal resources and herbivore standing crops are normally related in streams (see reviews by Gregory, 1983; Lamberti & Moore, 1984), and similarities in scraper biomass between streams may be attributed to similarities in density or composition of attached algae. Periphyton characteristics, however, were not examined in this study.

Unlike for the functional groups discussed above, taxonomic differences do not account for the significantly lower predator biomass and abundance in Huron River. The fact that scraper and collector-filterer abundance and biomass were also lowest in Huron River suggests that suitable prey may be less available in that stream.

Vertebrate taxa were not intentionally sampled in this study, however, all of the streams support large fish populations and some individuals were accidentally collected during invertebrate sampling. The northern mottled sculpin (*Cottus bairdi bairdi*) and slimy sculpin (*C. cognatus*) were common throughout the summer in the Salmon-Trout River and occurred, although less abundantly, in the other study streams. These predatory benthic fish play a significant role in the structure of the riffle community (e.g., Daiber, 1956; Soluk & Collins, 1988). Numerous sea lampreys (*Petromyzon marinus*) were observed spawning in erosional biotopes of the Salmon-Trout River during June. Nesting in this species includes the excavation of shallow depressions ca. 0.3 m in diameter in gravel substrate and thus certainly influences the microdistribution and abundance of benthic macroinvertebrates. In addition to sculpins, small catastomid and cyprinid fishes were collected, although infrequently, with other benthos in the Huron River. Longnose suckers (*Catastomus catastomus*) were very abundant in Pine River during the early summer sampling period. The observed population, by gross estimate, exceeded 300 mature individuals within the sampling area alone. The spawning and feeding behaviors of this fish (see Gilbert & Lee, 1980) significantly impact the macroinvertebrate fauna of erosional zones in the stream, at least during the late spring and early summer. No single fish species was notably conspicuous among the many seen in Mountain Stream.

Conclusion

The benthic assemblages examined appear generally similar in the four study streams in the Huron Mountains, but distributional patterns and functional data suggest that certain differences that do exist between streams may be related to factors associated with lake sources and distances from lake sources. Temperature, nutrient availability, and interspecific interactions are some parameters that require additional study in these systems. The results of this study offer a framework from which more detailed investigations of streams in the region may arise, and provide an adequate baseline for determining any future changes to these streams.

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