

RELATIONSHIPS BETWEEN BENTHIC ORGANIC MATTER AND
MACROINVERTEBRATES IN SAND SUBSTRATES
OF NORTHERN MICHIGAN STREAMS

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Abstract

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Relationships between benthic organic matter (BOM) and macroinvertebrates have been well studied in streams with coarse substrates, but such relationships have been little studied in sand habitats, despite the abundance of sand in many streams. These relationships were investigated in sand habitats of 15 streams in three watersheds of the Ottawa National Forest, Michigan. BOM size composition and macroinvertebrate biomass in sand habitats differed among the three watersheds. However, at this broad spatial scale, BOM quantity and quality had little effect on invertebrate community metrics in sand habitats. Sand-dwelling invertebrates were

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dominated by gathering- collectors, primarily Chironomidae, in all streams. A 32-day colonization experiment demonstrated that at a local scale BOM content of sand significantly affected macroinvertebrate abundance, biomass, and functional feeding group composition. BOM content of sand habitats likely represents one factor, among many components of this dynamic habitat, which shapes overall macroinvertebrate communities.

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CHAPTER 1

INTRODUCTION

1.1. Introduction

Quantifying the influence of energy and materials from the terrestrial/aquatic interface along riparian zones is crucial for improving the understanding of river ecosystem structure and function. In addition to maintaining microclimate conditions of streams and stabilizing banks (Murphy and Meehan 1991), riparian zones supply stream biota with allochthonous inputs that comprise an important source of energy for stream food webs, especially in small, forested streams or in large, turbid or deep rivers where autotrophic production is limited (Vannote et al. 1980). Allochthonous inputs contribute to the pool of benthic organic matter (BOM), which is a major food resource for stream invertebrates and some fishes (Minshall 1967; Anderson and Sedell 1979; Wallace et al. 1997; Hall et al. 2000). The composition of stream macroinvertebrate communities depends on many habitat variables such as food resources (e.g., Anderson and Cummins 1979), substrate (e.g., Minshall 1984), pH (e.g., Haines 1981), temperature (e.g., Vannote and Sweeney 1980), dissolved oxygen (e.g., Williams and Hynes 1974), flow (e.g., Newbury 1984), and biotic interactions (e.g., Peckarsky 1984).

Previous studies have demonstrated a positive relationship between BOM and invertebrate community metrics such as abundance and biomass (e.g., Egglisshaw 1964; Rabeni and Minshall 1997; Culp et al. 1983). Experimental removal of BOM inputs has been shown to reduce invertebrate abundance and biomass (Wallace et al. 1997, 1999) and alter stream food webs (Hall et al. 2000). Invertebrates improve their fitness by seeking out BOM patches in detritus-limited systems (Wallace et al. 1999; Rowe and Richardson 2001) and prefer BOM with higher N content (Iversen 1974; Gayte and Fontvieille 1997). However, most observational and experimental studies on the relationship between BOM and invertebrates have focused on habitats with coarse substrates (e.g., Egglisshaw 1964; Rabeni and Minshall 1977; Culp et al. 1983), rather than on finer substrates such as sand (particles ranging from 63 μm to 2 mm).

In general, sand habitats have been understudied compared to cobble and gravel habitats (Soluk 1985), perhaps because of a study bias towards high-gradient streams with coarse substrates (Allan 1995). Sand is a common substrate in lower gradient streams, especially in areas with lacustrine geology such as areas in the upper midwestern U.S. (Heinrich 2001). Sand-dwelling invertebrate communities are usually very different from those associated with coarser substrates and commonly consist of chironomid midges, oligochaetes, and amphipods, which are adept at burrowing into sand. Although sand may be too unstable for some macroinvertebrate taxa (e.g., scrapers) that prefer cobble and gravel, BOM appears to become more easily entrained in subsurface zones of sand than in other stream substrates (Metzler and Smock 1990).

BOM incorporated into sand via retention in debris dams, pools, and backwater areas, or mixed into sand during flood-induced bed movement, may be processed more

slowly in sand than in other substrate types and thereby function as a long-term food resource (Tillman et al. 2003). Invertebrates associated with BOM patches in sand may also serve as an important food source for fish populations in sand-bottom streams (Benke et al. 1979; Coffman and Ferrington, Jr. 1996). Because BOM is an important energy source for stream food webs (e.g., Minshall 1967; Hall et al. 2000), BOM may influence overall productivity in streams with sand habitats.

1.2. Research Objectives

The purpose of this thesis research was to investigate the relationship between BOM and invertebrates in sand habitats of low-gradient streams and to determine whether BOM quantity influenced invertebrate colonization (Figure 1.1). My primary hypothesis was that invertebrate community metrics would be positively related to BOM quantity and quality, because of the importance of BOM as a food resource for invertebrates. I further hypothesized that higher BOM quantity would result in higher rates of invertebrate colonization of sand habitats. I used a combination of observational studies and a field experiment to address these hypotheses.

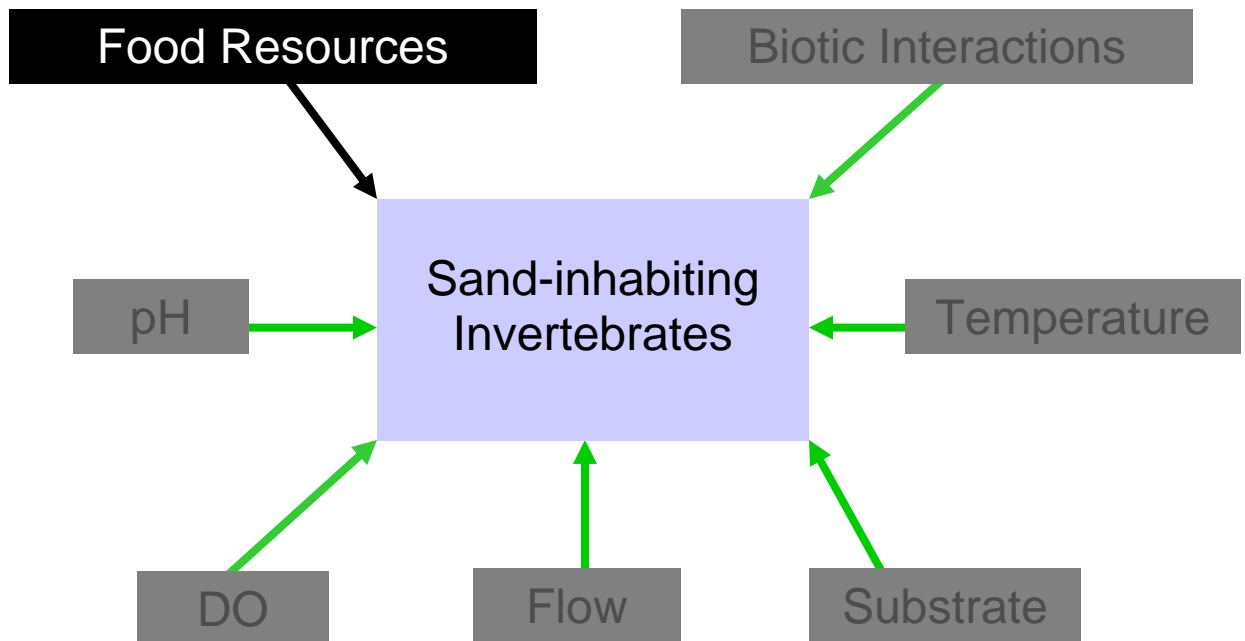


Figure 1.1. Simplified conceptual diagram of factors that influence the distribution of stream benthic invertebrates in sand habitats. Food resources (black box) may have greater relative effects on habitat suitability in sand habitats and are the focus of this study. DO=dissolved oxygen.

1.3. Study Site

All studies were conducted in streams located either within or directly adjacent to the Ottawa National Forest (ONF). The ONF is approximately 400,000 hectares of mostly regrowth forest located in the western Upper Peninsula of Michigan, which extends from the south shore of Lake Superior down to Wisconsin (USDA Forest Service 2004). Seasons range from severe winters, with some areas receiving over 500 cm of snow annually, to warm summers with sporadic precipitation. ONF aquatic habitats include approximately 20 kilometers of Lake Superior shoreline, over 500 lakes, and nearly 3,200 km of rivers and streams.

My research focused on 15 streams distributed among three watersheds of comparable size in the ONF: the Black-Presque Isle Rivers (area, 2,668 km²), the Ontonagon River (3,600 km²), and the Sturgeon River (1,839 km²) (Alexander et al. 1996). The 15 streams ranged widely in bankfull width (2.3 to 12.0 m), median substrate (sand to cobble), canopy cover (12 to 95%), sand composition (3 to 90% of total substrate), and average slope (0.2 to 1.8%).

1.4. Approach

My study consisted of two major components. First, I sampled sand habitats in the 15 study streams for BOM and benthic macroinvertebrates. BOM (all organic matter >45 µm) and invertebrates (animals >250 µm) were separated from sediment cores taken from sandy areas of each of the 15 streams. To examine the relationship of BOM to

invertebrate community metrics, data were analyzed at two different scales – among streams and within streams. Specifically, statistical relationships were quantified between invertebrate abundance, biomass, taxa richness, and diversity and BOM quantity and quality. Second, a 32-day colonization experiment was conducted in a sand-dominated reach of one stream. I manipulated the quantity of BOM within in-situ chambers to determine whether BOM directly influenced invertebrate colonization patterns.

1.5. Significance

Sand habitats in streams are important to study because the Great Lakes region and other areas with lacustrine geologies have many sand-bed streams. Regardless of the natural geology or gradient, cool-water streams are often managed as gravel-bottomed trout streams for sport fisheries. Because better food quality (Richards and Bacon 1994) and spawning habitats (Chapman 1988) for trout are associated with gravel and cobble habitats, stream managers often add gravel and cobble to streams naturally lacking these substrates (e.g., Moerke et al. 2004). To protect these newly added habitats and prevent habitat degradation by fine substrates, sand traps may be dug upstream to slow flow and allow fine substrates to settle. Plunge pools may also be created to provide adult fish habitat and channel constrictions may be engineered to increase current velocity and route fine sediments downstream. However, the cost and effort of maintaining these enhancements, such as cleaning out sand traps, can be considerable, especially in areas with sandy soils. I sought to better understand the relationship between invertebrates and

BOM in these often-prevalent sand habitats. Resource managers should consider the role of sand habitats, and their biota, in stream ecosystems in areas of sand geology. The goal of this thesis is to provide this information for the ONF.

1.6. Literature Cited

Allan, J.D. 1995. Stream ecology: structure and function of running waters. Kluwer Academic Publishers, Boston.

Alexander, R.B., J.R. Slack, A.S. Ludtke, K.K. Fitzgerald, T.L. Schertz, L.I. Briel, and K.P. Buttleman. 1996. Boundary descriptions and names of regions, subregions, accounting units, and cataloging units. USGS Digital Data Series 37: Data from selected US Geological Survey National Stream Water-Quality Monitoring Networks (WQN).
http://water.usgs.gov/pubs/dds/wqn96cd/wqn/wa/huc_name.txt

Anderson, N.H., and K.W. Cummins. 1979. Influences of diet on life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36:335-342.

Anderson, N.H., and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24:351-377.

Benke, A.C., D.M. Gillespie, F.K. Parrish, T.C. Van Arsdall, R.J. Hunter, and R.L. Henry. 1979. Biological basis for assessing impacts of channel modifications; invertebrate production, drift and fish feeding in a Southeastern blackwater river. Environmental Resource Center, Georgia Institute of Technology, Atlanta Report No. 06-79.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117:1-21.

Coffman, W.P., and L.C. Ferrington, Jr. 1996. Chironomidae. Pages 635-754 in Merritt, R.W., and K.W. Cummins (eds.). *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt, Dubuque, IA.

Culp, J.M., S.J. Walde, and R.W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1568-1574.

- Egglshaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *The Journal of Animal Ecology* 33:463-476.
- Gayte, X., and D. Fontvieille. 1997. Autochthonous vs. allochthonous organic matter ingested by a macroinvertebrate in headwater streams: *Gammarus* sp. as a biological probe. *Archiv für Hydrobiologie* 140:23-36.
- Haines, T.A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. *Transactions of the American Fisheries Society* 110:669-707.
- Hall, R.O., J.B Wallace, and S.L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81:3445-3463.
- Heinrich, E.W. 2001. Economic geology of the sand and sandstone resources of Michigan. Michigan Department of Environmental Quality Geological Survey Division. Report of Investigation 21. Lansing, MI 48909.
- Iversen, T.M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos* 25:278-282.
- Metzler, G.M., and L.A. Smock. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* 48:139-149.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. Pages 358-400 in Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Moerke, A.H., K.J. Gerard, J.A. Latimore, R.A. Hellenthal, and G.A. Lamberti. 2004. Restoration of an Indiana, USA, stream: bridging the gap between basic and applied lotic ecology. *Journal of the North American Benthological Society* 23:647-660.
- Murphy, M.L., and W.R. Meehan. 1991. River ecology and management in the Pacific coastal ecoregion. Pages 17-46 in Meehan, W.R. (ed.) *Influences of forest and rangeland management of salmonid fishes and their habitats*. American Fisheries Society, Bethesda, MD.
- Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. Pages 323-357 in Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.

- Peckarsky, B.L. 1984. Predator-prey interactions among aquatic insects. Pages 196-254 in Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Rabeni, C.F., and G.W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Richards, C., and K.L. Bacon. 1994. Influence of fine sediment on macroinvertebrate colonization of surface and hyporheic stream substrates. *Great Basin Naturalist* 54:106-113.
- Rowe, L., and J.S. Richardson. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. *Oecologia* 129:473-480.
- Soluk, D.A. 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1296-1302.
- Tillman, D.C., A.H. Moerke, C.L. Ziehl, and G.A. Lamberti. 2003. Subsurface hydrology and degree of burial affect mass loss and invertebrate colonization of leaves in a woodland stream. *Freshwater Biology* 48:98-107.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vannote, R.L., and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* 115:667-695.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409-442.
- Williams, D.D., and H.B.N. Hynes. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology* 4:233-256.
- USDA Forest Service (United States Department of Agriculture, Forest Service). October 19, 2004. Ottawa National Forest. <http://www.fs.fed.us/r9/ottawa/> October 23, 2004.

CHAPTER 2

MACROINVERTEBRATE COMMUNITIES AND BENTHIC ORGANIC MATTER IN SAND HABITATS OF 15 NORTHERN MICHIGAN STREAMS

2.1. Abstract

In streams with coarse substrates (e.g., cobble, gravel), increases in invertebrate abundances have been related to increases in food resources, such as benthic organic matter (BOM). However, this relationship has been little studied in streams with fine substrates, such as sand, despite the prevalence of sand in many streams, especially in lacustrine geologies. We hypothesized that sand habitats with higher BOM quantity and quality would have higher invertebrate abundance, biomass, taxa richness, and diversity. Sediment cores were taken from sand habitats of 15 streams within three watersheds of the Ottawa National Forest, Upper Peninsula, Michigan. Sand habitats in the 15 streams varied widely in mean total BOM quantity (112 to 1814 g AFDM·m⁻²) and size composition [very fine BOM (VFBOM, 0.45-250 μm), 0-58%; fine BOM (FBOM, 250 μm-1 mm), 11-27%; coarse BOM (CBOM, >1 mm), 27-81%] but differences were still detected among watersheds (VFBOM, ANOVA, $F_{2,11} = 8.69$, $p = 0.005$; CBOM, $F_{2,11} = 11.15$, $p=0.002$). Streams in the Black-Presque Isle Rivers watershed had more VFBOM

and less CBOM than streams in the Ontonagon River (VFBOM, Tukey's test, $p = 0.011$; CBOM, Tukey's $p = 0.006$) and Sturgeon River watersheds (VFBOM, Tukey's $p = 0.007$; CBOM, Tukey's $p = 0.003$). However, invertebrate biomass and individual size in streams in the Sturgeon River watershed tended to be higher than in streams in the Black-Presque Isle Rivers (biomass, Tukey's $p = 0.067$; individual size, Tukey's $p = 0.023$) and Ontonagon River watersheds (biomass, Tukey's $p = 0.061$; individual size, Tukey's $p = 0.019$). Some similarities were found among the 15 streams. Invertebrate abundance and biomass overall were dominated by gathering-collectors. Midge larvae of the family Chironomidae, most of which are gathering-collectors, comprised the major proportion of the invertebrates in both abundance ($73.6 \pm 15.4\%$; mean \pm SE; $n = 15$) and biomass ($56.2 \pm 18.8\%$; $n = 15$). Invertebrate abundance, biomass, taxa richness, and diversity were not significantly related to either BOM quantity or quality measures. Our results indicate that BOM and invertebrate community metrics in sand habitats differed among watersheds, but that invertebrate community metrics were not clearly related to BOM quantity and quality in these streams. Increasing the number of studies in this common, but understudied, habitat will improve our overall understanding of stream ecosystems, particularly in low gradient midwestern streams.

2.2. Introduction

The composition of stream macroinvertebrate communities depends on many habitat variables such as substrate (e.g., Minshall 1984), pH (e.g., Haines 1981), temperature (e.g., Vannote and Sweeney 1980), dissolved oxygen (e.g., Williams and

Hynes 1974), flow (e.g., Newbury 1984), biotic interactions (e.g., Peckarsky 1984), and food resources (e.g., Anderson and Cummins 1979). Among food resources, benthic organic matter (BOM) is a major component of the stream resource base to which invertebrates respond (Minshall 1967; Anderson and Sedell 1979; Wallace et al. 1999). For example, macroinvertebrate abundances declined (Wallace et al. 1997, 1999) and food webs changed (Hall et al. 2000) in streams where coarse BOM (CBOM, >1 mm) sources were excluded. In coarse sediments, increased BOM quantity can positively affect the abundance of lotic invertebrates (Eglishaw 1964; Rabeni and Minshall 1977; Culp et al. 1983). In detritus-limited systems, invertebrates may seek out BOM patches (Wallace et al. 1999; Rowe and Richardson 2001).

Because detritus varies in chemical composition and degree of conditioning (Petersen and Cummins 1974; Suberkropp et al. 1976; Golladay et al. 1983; Webster and Benfield 1986; Golladay and Sinsabaugh 1991), the quality of CBOM may also influence invertebrate communities. For example, Gayte and Fontvieille (1997) found that amphipods preferentially fed on CBOM with a low C:N ratio. In another study, caddisfly assimilation efficiency and food preference were positively related to leaf N content (Iversen 1974). We studied whether invertebrate community metrics were related to BOM quantity and quality in sand habitats of streams. Most previous studies have focused on invertebrate-BOM relationships in cobble or gravel, whereas few have investigated relationships in sand (i.e., particles ranging from 63 μm to 2 mm) habitat.

Because BOM is the base of many stream food webs (e.g., Minshall 1967; Hall et al. 2000), BOM entrained in sand habitats may influence overall stream biotic productivity. Sand habitats are common, and sometimes dominant, features in streams

with lacustrine geologies, such as in the Great Lakes region of the midwestern U.S. (Heinrich 2001) and have been understudied compared to gravel and cobble habitats (Soluk 1985). Several studies suggest that sand has lower invertebrate production and biomass than other stream substrates (Benke et al. 1984; Soluk 1985). However, sand-inhabiting invertebrates may still be an important food resource for fish populations (Benke et al. 1979; Coffman and Ferrington, Jr. 1996). Because low food resources in unstable sand habitats may limit invertebrate growth compared to coarser substrates (Soluk 1985), patches of BOM in sand may be critical to invertebrate growth. BOM appears to be more easily entrained in subsurface zones of sand than in other stream substrates. For example, 21% of allochthonous leaf input became buried in a sand-bottom first-order stream, which was three to 20 times more subsurface storage than in the coarse sediments of higher gradient streams (Metzler and Smock 1990). BOM processing also may be slower in sand than in other substrates (Metzler and Smock 1990; Tillman et al. 2003) thereby functioning as a long-term food resource. Therefore, invertebrates may interact differently with BOM in sand than in other substrates.

We related invertebrate abundance, biomass, diversity, and functional feeding group composition to BOM quantity and quality in sand habitats of 15 streams in the Upper Peninsula of Michigan, U.S.A. We assessed relationships at two different scales, among streams and within streams. We expected to find a positive relationship between the invertebrate metrics and BOM quantity and quality in sand habitats.

2.3. Methods

We studied 15 streams distributed across three watersheds of similar sizes (Black-Presque Isle Rivers = 2668 km², Ontonagon River = 3600 km², Sturgeon River = 1839 km²; Alexander et al. 1996) in the Ottawa National Forest, Upper Peninsula, Michigan (Figure 2.1). Study streams ranged widely in their size, canopy cover, time since last logged, and substrate composition (Table 2.1). Physical variables were measured during the summer of 2002 and 2003. BOM and invertebrate samples from sand habitats of all 15 streams were collected between July 10 and 19, 2003. Stream discharge was measured on the same day BOM and invertebrate samples were taken.

Sediment samples were collected from sandy areas of the streambed using a PVC corer (7.7 cm diameter, 10.0 cm deep; 466 cm³). One core was removed from a randomly determined location of sand habitats within each of five subsections of a 100-m stream reach. Five core samples were taken from each stream with the exception of State Creek, Shane Creek, and Walton Creek where 10 cores were collected. We considered two reaches of Two-Mile Creek (separated by >4 km) to be separate sites. Means of the samples were used in regression models.

2.3.1. *BOM Processing*

For each core, the BOM and invertebrates were elutriated five times through stacked sieves (1-mm and 250- μ m mesh) to separate coarse BOM from fine BOM (FBOM, 250 μ m-1 mm), and very fine BOM (VFBOM, 0.45-250 μ m). A subsample of the fines that passed through the sieves was collected and filtered onto a pre-ashed and

pre-weighed glass-fiber filter (0.45- μ m pore size). With the exception of a known quantity of CBOM set aside for later C and N analyses, all size fractions of BOM were dried (60 °C for 48 hr), weighed for dry mass, ashed (550 °C for 5 hr), and re-weighed to determine ash-free dry mass (AFDM) for the entire core after invertebrates were removed (modified from Wallace et al. 1982; Wallace and Grubaugh 1996). BOM quantity was reported as mass per area (e.g., Smock 1990). The CBOM subsample for C and N analysis was dried, homogenized by grinding, and then analyzed on a CHN analyzer (Costech Instruments® Elemental Combustion System® 4010 CHNS-O analyzer) to estimate C:N ratio and %N as measures of BOM quality.

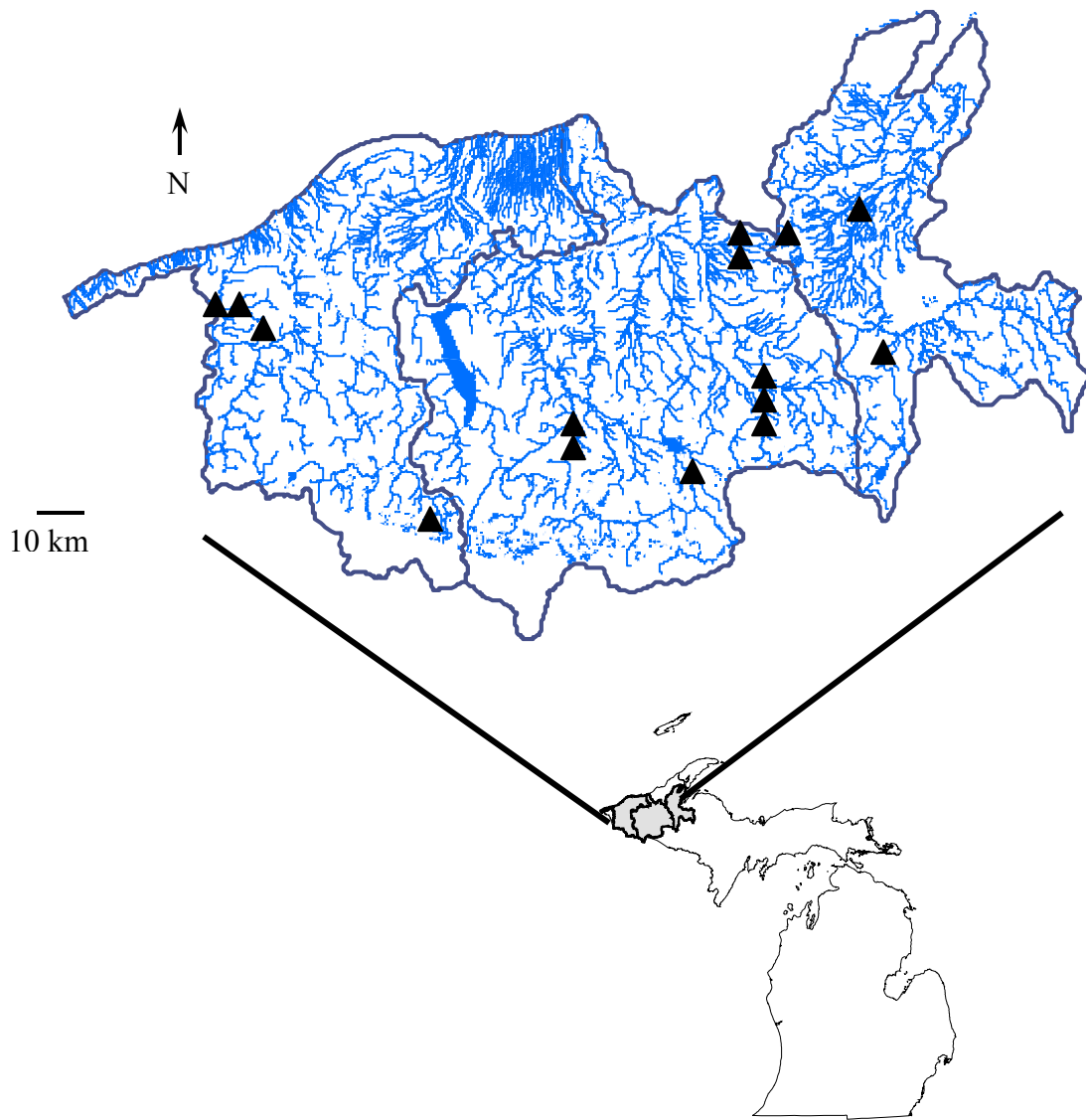


Figure 2.1. Map of 15 streams sampled within three watersheds (Black-Presque Isle, Ontonagon, Sturgeon) of the Ottawa National Forest, Upper Peninsula, MI.

TABLE 2.1.

CHARACTERISTICS OF 15 STUDY STREAMS WITHIN THE OTTAWA NATIONAL FOREST, UPPER PENINSULA, MI

Stream	Watershed	Latitude	Longitude	Years Last Logged	Bankfull width (m)	Discharge (m ³ ·sec ⁻¹)	Substrate (D ₅₀)	Canopy Cover (%)	Sand (%)	Slope (%)	Land Type Association
E. Branch Presque Isle	Black-Presque Isle	46 16' 35.4"	89 35' 34.3"	1936, 1940	9.4	0.17	pebble	16	13	1.30	Terminal moraine, coarse texture
Montowibo	Black-Presque Isle	46 33' 05.2"	90 00' 31.7"	1925	4.5	0.01	pebble	66	3	0.72	Ground moraine, coarse textured
Narrows	Black-Presque Isle	46 33' 40.5"	90 04' 41.7"	1910, 1915, 1926	5.9	0.02	pebble	77	4	0.88	Ground moraine, coarse textured
Reed	Black-Presque Isle	46 34' 17.0"	90 05' 13.7"	1910, 1925, 1935	4.0	0.04	pebble	80	7	0.97	Ground moraine, coarse textured
Jug	Ontonagon	46 41' 26.0"	88 58' 09.6"	1937, 2001	3.9	0.09	sand	79	90	0.83	Lake plains, coarse to medium textured
Leveque	Ontonagon	46 40' 04.7"	88 56' 53.8"	1934, 1940	4.3	0.07	gravel	69	17	0.75	Outwash plains, coarse textured
McGinty	Ontonagon	46 21' 19.7"	89 03' 09.3"	1924, 1934, 1940	5.0	0.06	gravel	52	31	0.43	Terminal moraine, coarse texture
State	Ontonagon	45 24' 49.1"	87 54' 20.3"	1918, 1922, 1924, 1967	2.4	0.06	pebble	90	19	1.83	Terminal moraine, coarse texture
Shane	Ontonagon	45 27' 51.8"	87 53' 46.4"	1932, 1947, 1967	2.8	0.04	sand	95	35	0.9	River valley and lake plain, Coarse to fine texture
Two-Mile (1)	Ontonagon	46 21' 51.5"	89 19' 52.6"	1930, 1938	9.4	0.06	pebble	25	20	0.56	Terminal moraine, coarse texture
Two-Mile (2)	Ontonagon	46 23' 10.2"	89 18' 53.1"	1895, 1987	12.0	0.16	cobble	79	13	0.64	Terminal moraine, coarse texture
Walton	Ontonagon	45 26' 44.8"	87 54' 36.3"	1912, 1915	2.3	0.03	sand	67	43	1.01	Recessional moraine, coarse textured
Perch	Sturgeon	46 31' 47.4"	88 39' 07.8"	1804, 1840, 1870	11.2	0.58	pebble	12	15	0.24	Ground moraine, fine textured
Silver	Sturgeon	46 43' 19.7"	88 44' 02.8"	1880, 1885, 1890, 1912	10.1	0.14	sand	61	70	0.26	Ground moraine, fine textured
W. Branch Sturgeon Tributary	Sturgeon	46 41' 38.9"	88 52' 55.9"	1927	4.5	Not detectable	sand	19	61	0.34	Terminal moraine, fine textured

2.3.2. *Invertebrate Processing*

Invertebrates (>250 μm) were elutriated from the core sample, live-picked from the BOM, and preserved in 7% formalin. Invertebrates were identified to the lowest taxonomic level possible (Pennak 1989; Hilsenhoff 1995; Merritt and Cummins 1996a), and measured for length to the nearest 0.5 mm under a stereomicroscope at 100X. Invertebrate biomass (as dry mass) was calculated using length-mass regressions (Benke et al. 1999; J.B. Wallace unpublished data). Invertebrate abundance and biomass were reported per area (e.g., Benke et al. 1984; Soluk 1985). Functional feeding groups (FFG) were assigned using Merritt and Cummins (1996a) and Pennak (1989) and apportioned by total invertebrate abundance and biomass per core. Taxa richness and Shannon-Weaver diversity (H') (Dodds 2002) were determined for each core.

2.3.3. *Statistical Analyses*

Among-stream and within-stream comparisons were made to determine whether invertebrate-BOM relationships varied at different scales. Among-stream comparisons were made using all 15 streams. From the largest watershed (Ontonagon River), within-stream comparisons were made for three streams that were similar in size and located in close proximity to each other. These streams also had the largest sample size ($n = 10$ per stream) from which to discern within-stream relationships. One-way ANOVA was used to compare BOM and invertebrate variables among watersheds (SYSTAT 10; SPSS Inc., 2000). Multiple comparisons (Tukey's HSD test) were conducted when significant differences were observed with ANOVA. Multiple linear regressions were conducted using BOM quantity, C:N ratio, and %N as independent variables and invertebrate abundance, biomass, taxa richness, and diversity as dependent variables. When

applicable, data were log- or square-root transformed to correct for non-normality before regressions were computed. Significance was determined at $\alpha = 0.05$.

2.4. Results

2.4.1. *BOM Quantity and Size Composition*

Sand habitats in the 15 streams varied widely in mean total BOM quantity (112 to 1814 g AFDM·m⁻²) and size composition (VFBOM, 0-58%; FBOM, 11-27%; CBOM, 27-81%) (Figure 2.2). VFBOM in streams in the Black-Presque Isle Rivers (39.9 ± 11.3%; mean ± SE; n = 4) watershed tended to be higher than in streams in the Ontonagon River (22.9 ± 4.4%; n = 8) or Sturgeon River (14.1 ± 7.5%; n = 3) watersheds ($F_{2,12} = 2.60$, $p = 0.116$). When Narrows Creek, an apparent outlier, was excluded from the analysis, VFBOM differed significantly among watersheds ($F_{2,11} = 8.69$, $p = 0.005$). Narrows Creek may have been an outlier because the reach Creek surveyed was noticeably closer to the confluence with the Black River than the other streams surveyed in the Black-Presque Isle watershed. This close proximity to a large river may highly influence organic matter transport and retention such as in the event of floods. Streams within the Black-Presque Isle Rivers watershed had significantly higher proportions of VFBOM (50.9 ± 3.8%; n = 3) than streams within the Ontonagon River watershed (Tukey's test, $p = 0.011$) or Sturgeon River watershed (Tukey's $p = 0.007$). In general, CBOM in streams in the Ontonagon River (59.1 ± 3.5%; n = 8) and Sturgeon River watersheds (68.3 ± 6.6%; n = 3) tended to be higher than in streams in the Black -Presque Isle Rivers watershed (44.1 ± 11.8%; n = 4) ($F_{2,12} = 2.49$, $p = 0.125$). When Narrows

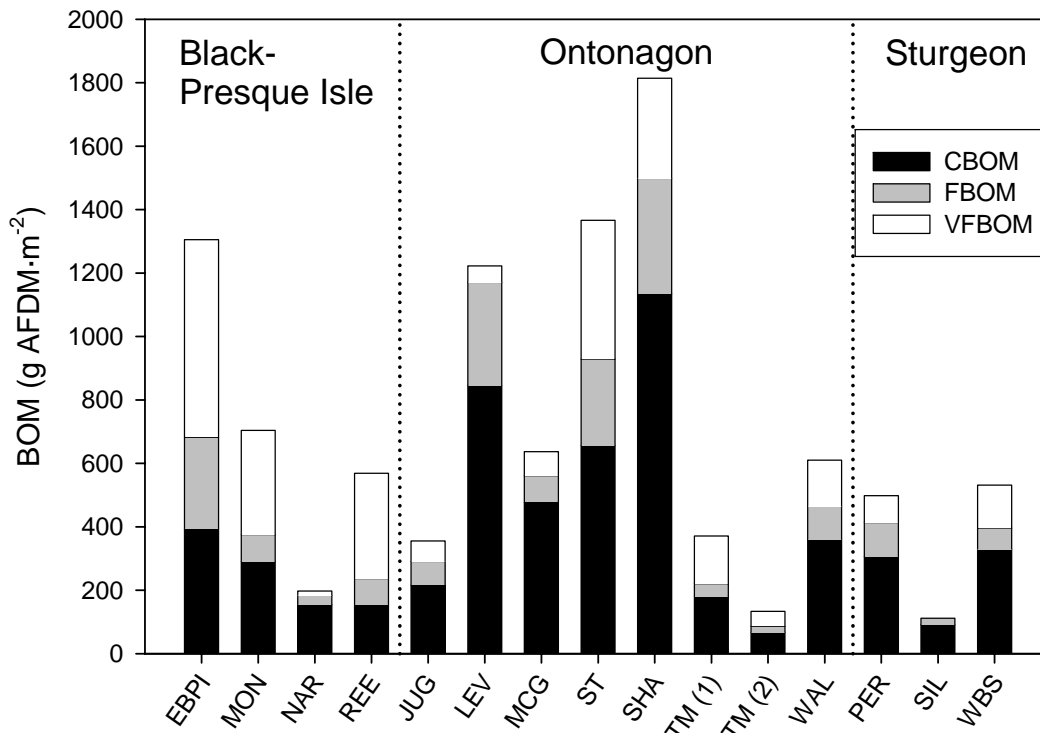


Figure 2.2. Mean benthic organic matter (BOM) quantity showing size fractions (coarse, C; fine, F; very fine, VF) for 15 streams in the Upper Peninsula, MI, in July 2003. EBPI = East Branch Presque Isle, MON = Montowibo, NAR = Narrows, REE = Reed, JUG = Jug, LEV = Leveque, MCG = McGinty, ST = State, SHA = Shane, TM (1) = Two-Mile (1), TM (2) = Two-Mile (2), WAL = Walton, PER = Perch, SIL = Silver, WBS = West Branch Sturgeon Tributary.

Creek was excluded, CBOM differed significantly among watersheds ($F_{2,11} = 11.15$, $p=0.002$). Streams within the Ontonagon River (Tukey's $p = 0.006$) and Sturgeon River (Tukey's $p = 0.003$) watersheds had significantly higher proportions of CBOM than streams within the Black-Presque Isle Rivers watershed ($32.7 \pm 4.4\%$; $n = 3$).

2.4.2. *Invertebrate Abundance, Biomass, and Functional Feeding Group Composition*

In sand habitats, mean invertebrate abundance (3,049 to 25,854 individuals·m⁻²; Figure 2.3) and biomass (109 to 3974 mg DM·m⁻²; Figure 2.4) varied widely among streams. Invertebrate abundance did not differ significantly among watersheds ($F_{2,12} = 0.52$, $p = 0.609$). However, invertebrate biomass differed significantly among watersheds ($F_{2,12} = 3.89$, $p = 0.050$). Streams in the Sturgeon River watershed ($2,646.4 \pm 1,268.2$ mg DM·m⁻²; mean \pm SE; $n = 3$) tended to have more biomass than in streams in the Black-Presque Isle Rivers (676.4 ± 192.1 mg DM·m⁻²; $n = 4$) (Tukey's $p = 0.067$) and Ontonagon River watersheds (861.0 ± 218.9 mg DM·m⁻²; $n = 8$) (Tukey's $p = 0.061$). Similarly, on average, invertebrate body size differed significantly among watersheds ($F_{2,12} = 6.12$, $p = 0.015$). More larger-bodied invertebrates were found in streams in the Sturgeon River watershed (0.189 ± 0.080 mg DM·individual⁻¹; $n = 3$;) than in streams in the Black-Presque Isle Rivers (0.045 ± 0.006 mg DM·individual⁻¹) (Tukey's $p = 0.023$) and Ontonagon River watersheds (0.057 ± 0.010 mg DM·individual⁻¹) (Tukey's $p = 0.019$). This difference can be attributed to the presence of large dragonfly larvae (Odonata) in Perch River and large oligochaete worms in the West Branch Sturgeon tributary, both located within the Sturgeon River watershed.

Invertebrates in sand were dominated numerically by gathering-collectors in all streams ($82.7 \pm 3.1\%$ of total invertebrates; $n = 15$; Figure 2.3, Appendix 1).

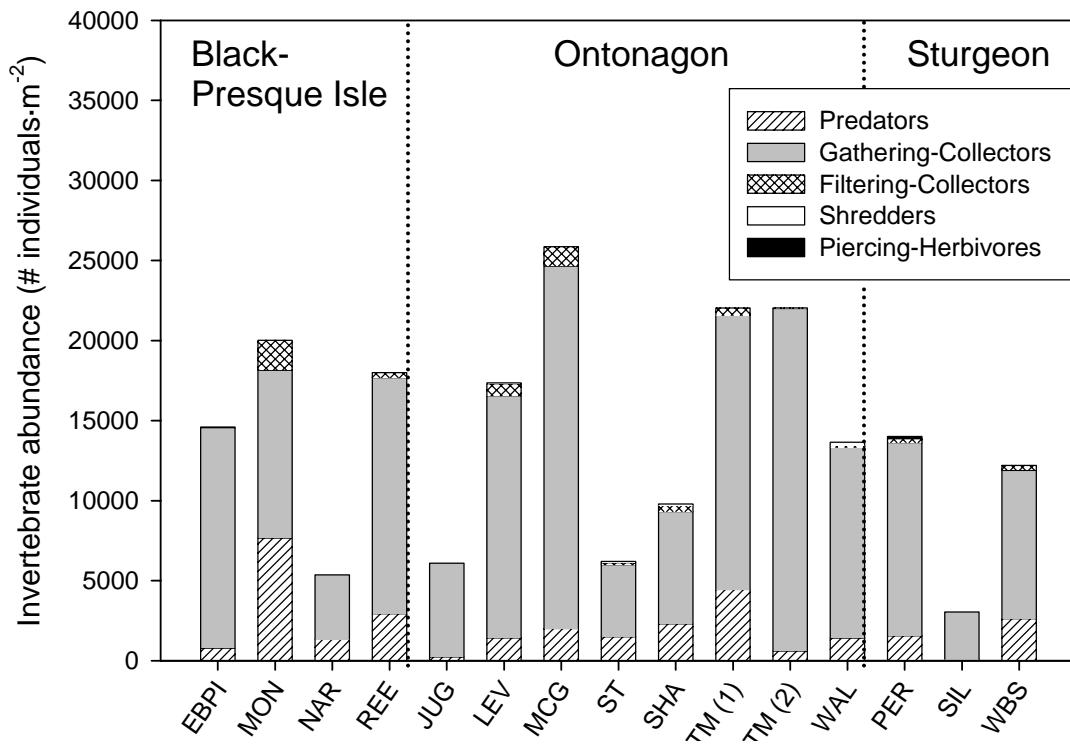


Figure 2.3. Mean invertebrate abundance showing functional feeding groups (FFG) for 15 streams in the Upper Peninsula, MI, in July 2003. EBPI = East Branch Presque Isle, MON = Montowibo, NAR = Narrows, REE = Reed, JUG = Jug, LEV = Leveque, MCG = McGinty, ST = State, SHA = Shane, TM (1) = Two-Mile (1), TM (2) = Two-Mile (2), WAL = Walton, PER = Perch, SIL = Silver, WBS = West Branch Sturgeon Tributary.

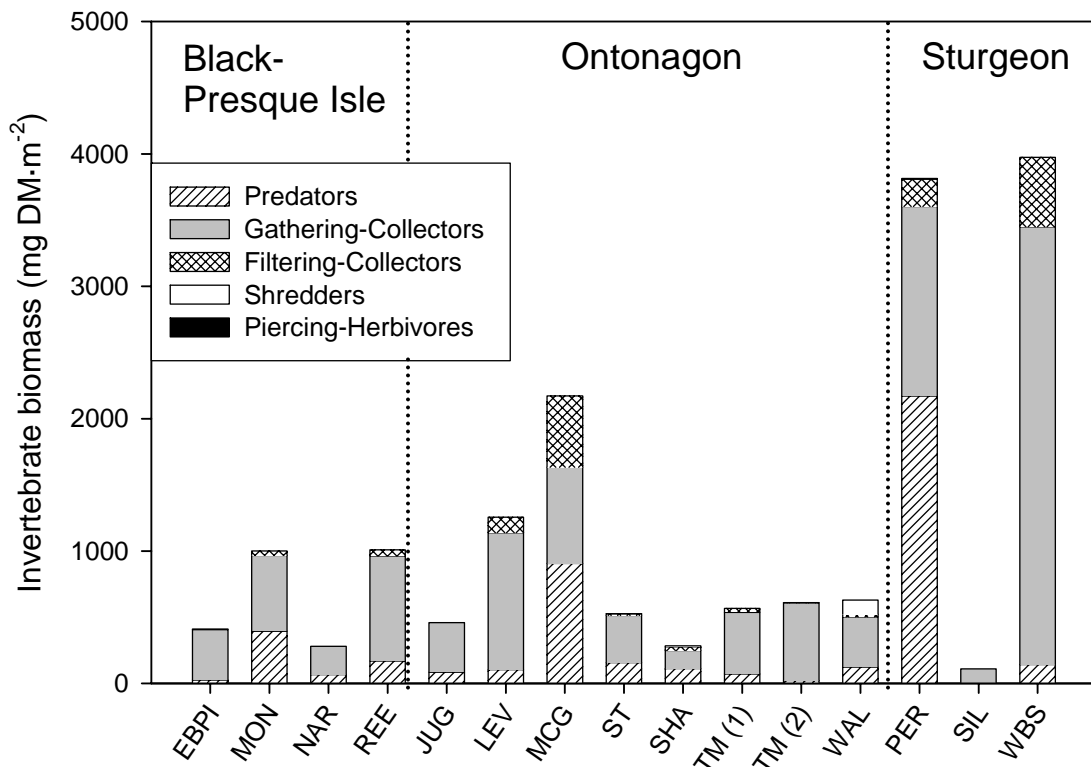


Figure 2.4. Mean invertebrate biomass showing functional feeding groups (FFG) for 15 streams in the Upper Peninsula, MI in July 2003. EBPI = East Branch Presque Isle, MON = Montowibo, NAR = Narrows, REE = Reed, JUG = Jug, LEV = Leveque, MCG = McGinty, ST = State, SHA = Shane, TM (1) = Two-Mile (1), TM (2) = Two-Mile (2), WAL = Walton, PER = Perch, SIL = Silver, WBS = West Branch Sturgeon Tributary.

Predators comprised the second highest proportion of invertebrate abundance overall ($14.7 \pm 2.7\%$; $n = 15$). Similarly, invertebrate biomass was dominated by gathering-collectors in most streams ($77.3 \pm 4.2\%$; $n = 13$) except for McGinty Creek and Perch River in which the greatest proportion of biomass consisted of predators (41.7% and 56.9%, respectively). Midge larvae of the family Chironomidae [subfamily Tanyptodinae, (predators), subfamilies Chironomini, Orthocladiinae, Diamesinae, Prodiamesinae, and Tanytarsini (gathering-collectors)] made up the major proportion of the invertebrates in both abundance ($73.6 \pm 15.4\%$; $n = 15$) and biomass ($56.2 \pm 18.8\%$; $n = 15$) (Appendix 2). Among-stream variability was high in taxa proportions of total invertebrate abundance and biomass (Figure 2.5). Midge larvae of the subfamilies Chironomini, Orthocladiinae, and Tanytarsini were present in all streams. Larger-bodied taxa such as Oligochaeta, Dipterans excluding the family Chironomidae, and Odonata tended to comprise larger proportions of total invertebrate biomass than abundance.

2.4.3. *Invertebrate Community Metrics and BOM Quantity and Quality*

In general, invertebrate abundance, biomass, taxa richness, and diversity were not linearly related to BOM quantity or quality in sand habitats across the 15 study streams (Table 2.2). Within the Ontonagon River watershed, we found weak relationships between some pairs of variables. Shannon-Weaver diversity was positively related to BOM C:N ratio in State Creek ($R^2 = 0.54$, $p = 0.009$) and invertebrate abundance was positively related to BOM C:N in Walton Creek ($R^2 = 0.45$, $p = 0.019$). Invertebrate taxa richness ($R^2 = 0.40$, $p = 0.029$) and diversity ($R^2 = 0.48$, $p = 0.016$) appeared to be negatively related to BOM quantity in Walton Creek, but this relationship was driven by one sample.

TABLE 2.2.

MULTIPLE REGRESSION RELATIONSHIPS BETWEEN INVERTEBRATE ABUNDANCE (INDIVIDUALS·M⁻²), BIOMASS (MG DM·M⁻²), TAXA RICHNESS, AND DIVERSITY AND BOM MASS (G AFDM·M⁻²), C:N RATIO, AND %N IN STREAMS IN THE UPPER PENINSULA, MI. PARTIAL ADJUSTED R²'S ARE REPORTED

Stream	n	Invertebrate variable	BOM mass		BOM C:N ratio		BOM %N	
			R ²	p	R ²	p	R ²	p
All Streams	15	Abundance	<0.01	>0.5	<0.01	>0.05	<0.01	>0.5
		Biomass	<0.01	>0.5	<0.01	>0.05	<0.01	>0.2
		Taxa richness	<0.01	>0.5	<0.01	>0.05	<0.01	>0.5
		S-W diversity index	<0.01	>0.5	<0.01	>0.05	<0.01	>0.2
State Creek	10	Abundance	<0.01	>0.2	<0.01	>0.5	<0.01	>0.05
		Biomass	<0.01	>0.2	<0.01	>0.5	<0.01	>0.1
		Taxa richness	<0.01	>0.1	<0.01	>0.1	<0.01	>0.1
		S-W diversity index	<0.01	>0.2	0.54	0.009	<0.01	>0.05
Walton Creek	10	Abundance	<0.01	>0.5	0.45	0.019	<0.01	>0.2
		Biomass	<0.01	>0.5	<0.01	>0.2	<0.01	>0.5
		Taxa richness	0.40	0.029	<0.01	>0.05	<0.01	>0.5
		S-W diversity index	0.48	0.016	<0.01	>0.1	<0.01	>0.5
Shane Creek	10	Abundance	<0.01	>0.2	<0.01	>0.5	<0.01	>0.2
		Biomass	<0.01	>0.5	<0.01	>0.5	<0.01	>0.05
		Taxa richness	<0.01	>0.5	<0.01	>0.5	<0.01	>0.2
		S-W diversity index	<0.01	>0.5	<0.01	>0.5	<0.01	>0.2
Among Cores								
From All Streams	88	Abundance	<0.01	>0.5	<0.01	>0.2	<0.01	>0.5
		Biomass	<0.01	>0.5	<0.01	>0.1	<0.01	>0.2
		Taxa richness	<0.01	>0.5	<0.01	>0.2	<0.01	>0.5
		S-W diversity index	<0.01	>0.5	<0.01	>0.2	<0.01	>0.5

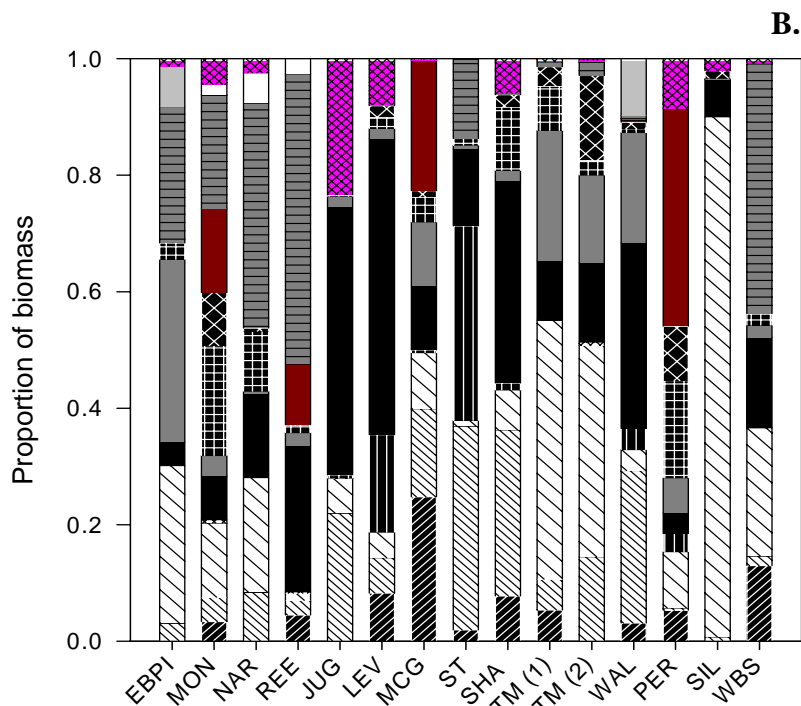
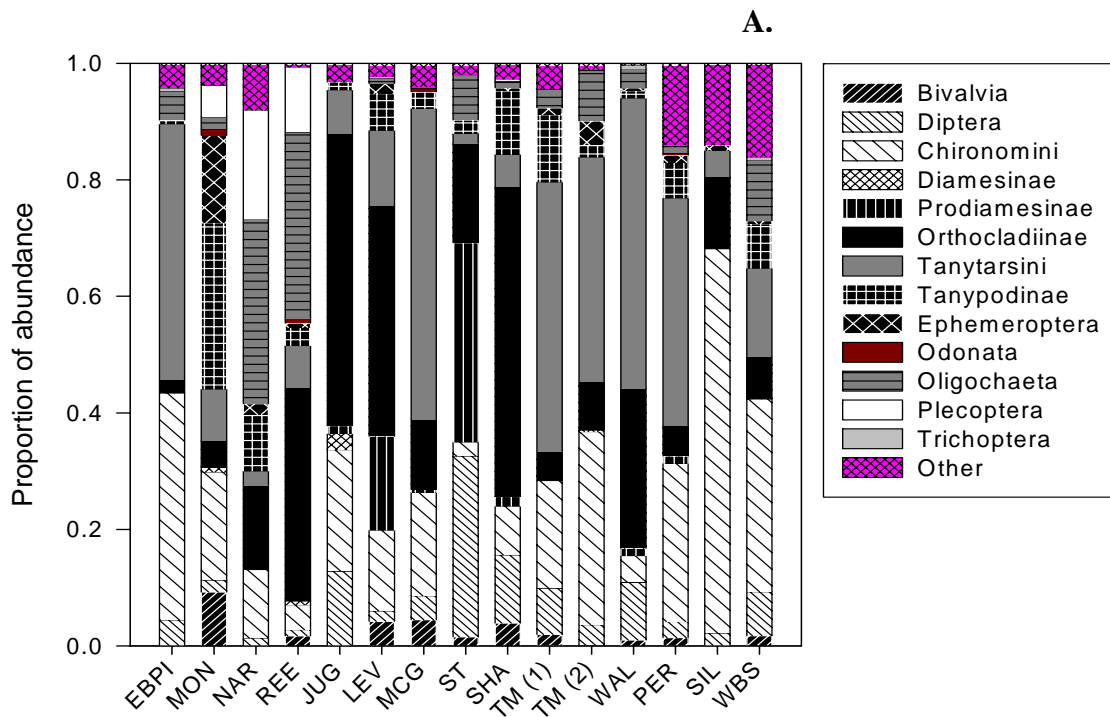


Figure 2.5. Taxa proportions of total invertebrate abundance (A) and biomass (B) for 15 streams in the Upper Peninsula, MI, in July 2003. EBPI = East Branch Presque Isle, MON = Montowibo, NAR = Narrows, REE = Reed, JUG = Jug, LEV = Leveque, MCG = McGinty, ST = State, SHA = Shane, TM (1) = Two-Mile (1), TM (2) = Two-Mile (2), WAL = Walton, PER = Perch, SIL = Silver, WBS = West Branch Sturgeon Tributary. ‘Diptera’ refers to all dipterans excluding the family Chironomidae. ‘Other’ refers to all invertebrates not belonging to any of the listed taxa.

2.5. Discussion

Differences in BOM composition and invertebrate biomass were detected among watersheds. Streams within the Black-Presque Isle Rivers watershed had more VFBOM and less CBOM than streams within the Ontonagon River or Sturgeon River watersheds. Because streams within the Black-Presque Isle Rivers watershed had generally larger substrate (D_{50} = pebble) than streams within the Ontonagon River or Sturgeon River watersheds (D_{50} = sand; Table 2.1), retention of FBOM may have increased in streams with coarser substrates leading to higher proportions of VFBOM following processing. For example, Rabeni and Minshall (1977) found fine detritus to be more abundant in trays with gravel and pebble substratum than in trays with other substratum sizes where smaller BOM may not have been as easily retained and allowed to accumulate. Total invertebrate biomass and individual size were higher in streams within the Sturgeon River watershed than in streams within the Black-Presque Isle Rivers or Ontonagon River watersheds. Even though this difference was driven by the presence of large dragonfly larvae in Perch River (PER) and long oligochaete worms in the West Branch Sturgeon tributary (WBS), these streams also had the highest Shannon-Weaver diversity indices (PER = 1.606, WBS = 1.633) among all study streams (1.337 ± 0.056 ; $n = 15$). Sand habitats of the Sturgeon River watershed appeared to contain more invertebrate taxa than the other study streams.

In general, sand habitats across all three watersheds and 15 streams appeared to provide better habitat for gathering-collectors than for other functional feeding groups. Sand habitats can be highly unstable and have less available oxygen than coarser substrates due to limited interstitial pore space (Allan 1995). Small, worm-like,

burrowing invertebrates such as midge larvae (Chironomidae) are adapted to living in sand habitats (Palmer and Strayer 1996; Wallace and Anderson 1996; Boulton 2000). Chironomids, most of which are gathering-collectors, are common inhabitants of sand habitats in streams (Benke et al. 1984; Soluk 1985; Palmer 1990). Some midge larvae construct burrows made from sand-grains, which extend to the surface of the substrate (Cummins and Merritt 1996).

In contrast, gathering-filterers were rare in sand habitats of the study streams. Gathering-filterers attach to substrate surfaces (Cummins and Merritt 1996), and therefore are ill adapted to shifting sand habitats. Typical macroinvertebrate shredders, such as *Tipula* (crane fly larvae) and *Lepidostoma* (caddisfly larvae), are generally large compared to midge larvae (e.g., Benfield et al. 1979; Merritt and Cummins 1996b), which may account for their low numbers in sand habitats. However, the larger predators that were present in our samples may be responding to relatively high prey densities in sand habitats (e.g., Peckarsky 1984) especially of chironomid midges.

In general, invertebrate abundance, biomass, taxa richness, and diversity in our study streams were not significantly related to either BOM quantity or quality measures as we had predicted. Our results contrast with other studies conducted with coarser sediments that found a positive relationship between invertebrate community metrics and BOM quantity (Eglishaw 1964; Rabeni and Minshall 1977; Culp et al. 1983; Drake 1984; Wallace et al. 1999) or quality (Pandian and Marian 1986). However, invertebrate abundance and diversity were positively related to increasing C:N ratio (i.e., declining BOM quality) in two study streams. Possibly, higher invertebrate abundance and diversity may lower BOM quality (i.e., increase BOM C:N ratio) via preferential feeding on more nutritional BOM (Peckarsky 1980; Golladay et al. 1983). Some invertebrates

eat just the mesophyll of leaves, while avoiding venation, which increases lignin and cellulose content while decreasing BOM quality (Suberkropp et al. 1976; Ward and Woods 1986). Due to widely varying among stream BOM source differences in the riparian zone tree composition (personal observation) and time since last logged (Table 2.1), BOM quantity and quality may have been influenced (Webster and Benfield 1986; Hutchens, Jr. and Wallace 2002). This in turn may have reduced the ability to detect patterns between invertebrate community metrics and BOM variables. Overall, the physical attributes of sand habitats may play a larger role in affecting invertebrate community metrics than the quantity and quality of food resources (Wallace and Anderson 1996).

We compared invertebrate abundance and biomass in sand habitats of Michigan streams with values from other North American studies. Invertebrate abundance in sand habitats of our study streams ranged from about 3000 to 26,000 individuals·m⁻² and biomass ranged from 100 to 4000 mg DM·m⁻². In Alberta streams, invertebrate abundances in sand habitats ranged from 12,000 to 78,000 individuals·m⁻² and biomass ranged from 50 to 490 mg DM·m⁻² (Soluk 1985). In a Georgia river, invertebrate abundances in sand habitats averaged >20,000 individuals·m⁻² and biomass was about 100 mg DM·m⁻² (Benke et al. 1984). In a Texas stream (Phillips 2003), mean invertebrate densities were low in sand (216 individuals·m⁻²) but mean taxa richness (26 taxa) was higher than in our Michigan streams (8 taxa on average). In two North Carolina streams (Wallace et al. 1999), invertebrate abundances were higher in mixed substrates of cobble, pebble, and sand-silt (62,252 and 37,670 individuals·m⁻² in the separate streams) than in sand habitats of our study streams, but their invertebrate biomass (1,815 and 1,002 mg AFDM·m⁻²) was comparable to sand habitats of our study

streams. Therefore, the Michigan streams that we studied contained abundances and biomasses of sand invertebrate assemblages that fall within the range of those found in other North American streams.

Accounting for differences in invertebrate community metrics of sand habitats within and among regions is important for researchers to consider, especially when generalizations are made about these habitats. Furthermore, production may be the most meaningful measure of sand-dwelling invertebrates that are often small and have rapid turnover (Benke et al. 1984). Biomass measures may underestimate the importance of the sand community on overall stream productivity, especially when comparisons are made with invertebrate communities of other habitat types. Further studies of invertebrate communities in sand habitats should focus on invertebrate production to more accurately estimate community impacts on overall stream dynamics.

Sand invertebrate communities should be considered when sampling streams with sand habitats because their impact on overall stream productivity may be significant. Streams with substantial sand habitat are common, especially in areas with lacustrine geologies and in watersheds with agricultural land use (Soil Survey Staff 1999). Our study demonstrated that BOM and invertebrate communities in sand habitats differ among watersheds. We also demonstrated that, unlike studies in coarser substrates, invertebrate community metrics had little relationship to BOM quantity or quality in sand habitats of our study streams. Because invertebrate community metrics in sand habitats vary substantially across regions, increasing the number of studies of this unique habitat will improve our overall understanding of stream ecosystems. Additional research is needed to better understand the factors important in determining community structure of sand-dwelling invertebrates.

2.6. Acknowledgments

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2.7. Literature Cited

- Alexander, R.B., J.R. Slack, A.S. Ludtke, K.K. Fitzgerald, T.L. Schertz, L.I. Briel, and K.P. Buttleman. 1996. Boundary descriptions and names of regions, subregions, accounting units, and cataloging units. USGS Digital Data Series 37: Data from selected US Geological Survey National Stream Water-Quality Monitoring Networks (WQN).
http://water.usgs.gov/pubs/dds/wqn96cd/wqn/wa/huc_name.txt
- Allan, J.D. 1995. Stream ecology: structure and function of running waters. Kluwer Academic Publishers, Boston, MA.

- Anderson, N.H., and K.W. Cummins. 1979. Influences of diet on life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36:335-342.
- Anderson, N.H., and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24:351-377.
- Benfield, E.F., R.W. Paul, and J.R. Webster. 1979. Influence of exposure technique on leaf breakdown rates in streams. *Oikos* 33:386-391.
- Benke, A.C., D.M. Gillespie, F.K. Parrish, T.C. Van Arsdall, R.J. Hunter, and R.L. Henry. 1979. Biological basis for assessing impacts of channel modifications; invertebrate production, drift and fish feeding in a Southeastern blackwater river. Environmental Resource Center, Georgia Institute of Technology, Atlanta Report No. 06-79.
- Benke, A.C., A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308-343.
- Benke, A.C., T.C. Van Arsdall, Jr., D.M. Gillespie, and F.K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25-63.
- Boulton, A. 2000. The subsurface macrofauna. Pages 337-361 *in* Jones, J.B., and P.J. Mulholland (eds.). *Streams and ground waters*. Academic Press, San Diego, CA.
- Coffman, W.P., and L.C. Ferrington, Jr. 1996. Chironomidae. Pages 635-754 *in* Merritt, R.W., and K.W. Cummins (eds.). *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt, Dubuque, IA.
- Culp, J.M., S.J. Walde, and R.W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1568-1574.
- Cummins, K.W., and R.W. Merritt. 1996. Ecology and distribution of aquatic insects. Pages 74-86 *in* Merritt, R.W., and K.W. Cummins (eds.). *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt Publishing Company, Dubuque, IA.
- Dodds, W.K. 2002. *Freshwater ecology: concepts and environmental applications*. Academic Press, San Diego, CA.
- Drake, J.A. 1984. Species aggregation: the influence of detritus in a benthic invertebrate community. *Hydrobiologia* 112:109-115.

- Egglisshaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *The Journal of Animal Ecology* 33:463-476.
- Gayte, X., and D. Fontvieille. 1997. Autochthonous vs. allochthonous organic matter ingested by a macroinvertebrate in headwater streams: *Gammarus* sp. as a biological probe. *Archiv für Hydrobiologie* 140:23-36.
- Gessner, M.O. 1999. A perspective on leaf litter breakdown in streams. *Oikos* 85:377-384.
- Golladay, S.W., and R.L. Sinsabaugh. 1991. Biofilm development on leaf and wood surfaces in a boreal river. *Freshwater Biology* 25:437-450.
- Golladay, S.W., J.R. Webster, and E.F. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. *Holarctic Ecology* 6:157-162.
- Haines, T.A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. *Transactions of the American Fisheries Society* 110:669-707.
- Hall, R.O., J.B Wallace, and S.L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81:3445-3463.
- Heinrich, E.W. 2001. Economic geology of the sand and sandstone resources of Michigan. Michigan Department of Environmental Quality Geological Survey Division. Report of Investigation 21. Lansing, MI 48909.
- Hilsenhoff, W.L. 1995. Aquatic insects of Wisconsin. Keys to Wisconsin genera and notes on biology, habitat, distribution, and species. University of Wisconsin Natural History Museums Council Pub. Coop. Ext. Publications #G3648, Room 245, 30 N. Murray St., Madison, WI 53715.
- Hutchens, Jr. J.J., and J.B. Wallace. 2002. Ecosystem linkages between southern Appalachian headwater streams and their banks: leaf litter breakdown and invertebrate assemblages. *Ecosystems* 5:80-91.
- Iversen, T.M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos* 25:278-282.
- Merritt, R.W., and K.W. Cummins (eds.). 1996a. An introduction to the aquatic insects of North America, 3rd ed. Kendall/Hunt, Dubuque, IA.
- Merritt, R.W., and K.W. Cummins. 1996b. Trophic relations of macroinvertebrates. Pages 453-474 in Hauer, F.R., and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego, CA.

- Metzler, G.M., and L.A. Smock. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* 48:139-149.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. Pages 358-400 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. Pages 323-357 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Palmer, M.A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *Journal of the North American Benthological Society* 9:17-25.
- Palmer, M.A., and D.L. Strayer. 1996. Meiofauna. Pages 315-337 *in* Hauer, F.R., and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego, CA.
- Pandian, T.J., and M. P. Marian. 1986. An indirect procedure for the estimation of assimilation efficiency of aquatic insects. *Freshwater Biology* 16:93-98.
- Peckarsky, B.L. 1980. Influence of detritus upon colonization of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 37:957-963.
- Peckarsky, B.L. 1984. Predator-prey interactions among aquatic insects. Pages 196-254 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Pennak, R.W. 1989. *Freshwater invertebrates of the United States*, 3rd ed. Wiley, New York.
- Petersen, R.C., and K.W. Cummins. 1974. Leaf processing in a woodland stream. *Freshwater Biology* 4:343-368.
- Phillips, E.C. 2003. Habitat preference of aquatic macroinvertebrates in an east Texas sandy stream. *Journal of Freshwater Ecology* 18:1-11.
- Rabeni, C.F., and G.W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Rowe, L., and J.S. Richardson. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. *Oecologia* 129:473-480.

- Smock, L.A. 1990. Spatial and temporal variation in organic matter storage in low-gradient, headwater streams. *Archiv für Hydrobiologie* 118:169-184.
- Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys, 2nd ed. United States Department of Agriculture, Washington, D.C.
- Soluk, D.A. 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1296-1302.
- Suberkropp, K., G.L. Godshalk, and M.J. Klug. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* 57:720-727.
- Tillman, D.C., A.H. Moerke, C.L. Ziehl, and G.A. Lamberti. 2003. Subsurface hydrology and degree of burial affect mass loss and invertebrate colonization of leaves in a woodland stream. *Freshwater Biology* 48:98-107.
- Vannote, R.L., and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* 115:667-695.
- Wallace, J.B., and N.H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 *in* Merritt, R.W., and K.W. Cummins (eds.). *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt Publishing Company, Dubuque, IA.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409-442.
- Wallace, J.B., and J.W. Grubaugh. 1996. Transport and storage of FPOM pp. 191-215 *in* Hauer, F.R. and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego.
- Wallace, J.B., D.H. Ross, and J.L. Meyer. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. *Ecology*. 63:824-838.
- Ward, G.M., and D.R. Woods. 1986. Lignin and fiber content of FPOM generated by the shredders *Tipula abdominalis* (Diptera: Tipulidae) and *Tallaperla cornelia* (Needham and Smith) (Plecoptera: Peltoperlidae). *Archiv für Hydrobiologie* 107:545-562.

- Webster, J.R., and E.F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.
- Williams, D.D., and H.B.N. Hynes. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology* 4:233-256.

CHAPTER 3

INFLUENCE OF ORGANIC MATTER ON INVERTEBRATE COLONIZATION OF SAND SUBSTRATE IN A NORTHERN MICHIGAN STREAM

3.1. Abstract

Sand is a common substrate in many streams, especially in lacustrine geologies, but has been less studied as a habitat for invertebrates than other substrates such as gravel and cobble. We hypothesized that benthic organic matter (BOM) content of sand would influence the abundance and community structure of macroinvertebrates in sand habitats. Levels of coarse BOM (no = 0; low = 1%; high = 5%, as dry mass) were manipulated within forty-five 539-cm³ colonization chambers implanted in a sand-dominated reach of Shane Creek, Ottawa National Forest, MI. Common insect colonizers of chambers were Chironomidae, Tipulidae, and Trichoptera. At the end of the 32-day experiment, invertebrate abundance (ANOVA, $F_{2,12} = 7.5$, $p = 0.015$) and biomass ($F_{2,12} = 8.7$, $p = 0.010$) were significantly higher in chambers with the low-BOM treatment than the no-BOM treatment, but the high-BOM treatment did not differ from the no-BOM treatment. Throughout the experiment, functional feeding groups (FFG) were numerically dominated by gathering-collectors in all treatments, but predators increased over time in the no-BOM and high-BOM treatments. At the beginning of the experiment, FFG

biomass was dominated by shredders. Over time, predator biomass increased in the no-BOM and high-BOM treatments. In general, taxa richness was higher in the low-BOM treatment than in the high-BOM treatment ($F_{2,108} = 4.1$, $p = 0.025$) whereas net community respiration was higher in the high-BOM treatment than in the low-BOM treatment ($F_{2,108} = 6.0$, $p = 0.006$). Our results suggest that the low-BOM treatment supported more invertebrates than the no and high-BOM treatments because of fewer predators and potentially higher biological oxygen availability. Therefore, local patterns of BOM accumulation may affect macroinvertebrate abundance and distributional patterns in sand habitats of forested streams.

3.2. Introduction

Macroinvertebrate colonization and community composition of habitat patches in streams are affected by chemical, physical, and biological factors including food resources (e.g., Anderson and Cummins 1979), biotic interactions (e.g., Peckarsky 1984), temperature (e.g., Vannote and Sweeney 1980), substrate (e.g., Minshall 1984), pH (e.g., Haines 1981), dissolved oxygen (e.g., Williams and Hynes 1974), and flow (e.g., Newbury 1984). Invertebrates colonize habitat patches via drift, upstream and downstream movement on the streambed, vertical migration, and adult oviposition (Williams and Hynes 1976) and are limited by mobility and life history features (e.g., Müller 1954, 1982). Habitats and associated chemical, physical, and biological features tend to be patchily distributed within a stream and range widely in their suitability for benthic fauna (Cummins and Lauff 1969; Minshall 1984; Palmer 1990).

We assessed whether food resource abundance altered habitat suitability for colonizing invertebrates in a sand-bottom stream. Benthic organic matter (BOM) is a major food resource for stream invertebrates (Wallace et al. 1997; Hall et al. 2001). Using gut content analyses, Bärlocher (1983) found that amphipods in a Swiss stream switched from a coarse particulate organic matter (CPOM) diet to that of fine POM (FPOM) depending on the season. Miyake and Nakano (2002) found that macroinvertebrate abundance and taxa richness were positively related to BOM standing crop. Invertebrates also have been shown to track accumulations of BOM such as in a reclaimed coal-mined river, where invertebrates colonized in synchrony with detrital accumulations. (Gore 1979, 1982). In detritus-limited systems, some invertebrates seek out BOM patches, which improves their fitness (Wallace et al. 1999; Rowe and Richardson 2001). At larger scales, manipulations to reduce detrital inputs have been shown to reduce invertebrate abundance and biomass (Wallace et al. 1997) and alter stream food webs (Hall et al. 2000).

Previous experimental studies have shown that BOM, when limiting, is positively associated with invertebrate abundances (Egglishaw 1964; Rabeni and Minshall 1977; Culp et al. 1983). However, these studies have focused on larger substrates, whereas none have examined finer substrates such as sand (particles ranging from 63 μm to 2 mm). Sand is an important substrate of streams worldwide (Soil Survey Staff 1999), but is less studied compared to other inorganic substrates such as gravel and cobble (Soluk 1985). Sand habitats in streams are especially common in lacustrine geologies, such as areas in the upper midwestern U.S. (Heinrich 2001). Although sand is unstable and supports lower invertebrate biomass and production than other substrates, such as gravel and cobble (Benke et al. 1984; Soluk 1985), sand-dwelling invertebrates may be an

important food source for fish populations of sand-bottom streams. Because low food abundance can limit the growth of sand-dwelling invertebrates (Soluk 1985), BOM buried in sand may improve habitat quality despite sand being prone to disturbance. Metzler and Smock (1990) estimated that 21% of the fall allochthonous leaf input became buried in a first-order, sand-bottom stream. In sandy reaches of a Michigan stream, invertebrates colonized buried leaf packs more slowly than leaf packs on the streambed, and leaves were processed more slowly in the subsurface zone which may function as a long-term OM retention site (Tillman et al. 2003). BOM may become incorporated into sand by being retained at debris dams, pools, and backwater areas, or mixed into sand during flood-induced bed movement.

While considerable research has addressed the independent effects of substrate type or organic matter content on benthic invertebrate colonization and distribution, relatively little is known how BOM content of sand habitats affects invertebrate colonization and community structure. Our study experimentally addressed whether the abundance of BOM altered the habitat suitability of sand for colonizing invertebrates. We determined whether BOM quantity affected invertebrate abundance, biomass, functional feeding group composition, taxa richness and diversity, and community respiration. We predicted a positive relationship between BOM quantity and invertebrate community characteristics and community respiration.

3.3. Study Site

We conducted a colonization experiment in Shane Creek (Houghton Co., MI; 46°28'N, 88°54'W, elevation 400 m) in the Upper Peninsula of Michigan. Shane Creek

is a small (mean $Q = 0.046 \text{ m}^3 \cdot \text{s}^{-1}$), low-gradient stream in the Ontonagon River watershed of the Ottawa National Forest (ONF) (Figure 3.1). The underlying geology of Shane Creek consists of terminal moraine overlain by deep, well-drained, coarse-textured soils (Ottawa National Forest 1986). The streambed sediments of Shane Creek are dominated by sand, followed by gravel, pebble, silt, and cobble (Table 3.1). Red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), eastern white pine (*Pinus strobes*), northern whitecedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*) are the most common riparian trees. Our experiment was conducted in a sand-dominated reach of Shane Creek. This reach was chosen because it was relatively uniform in stream width, depth, current velocity, and substrate composition.

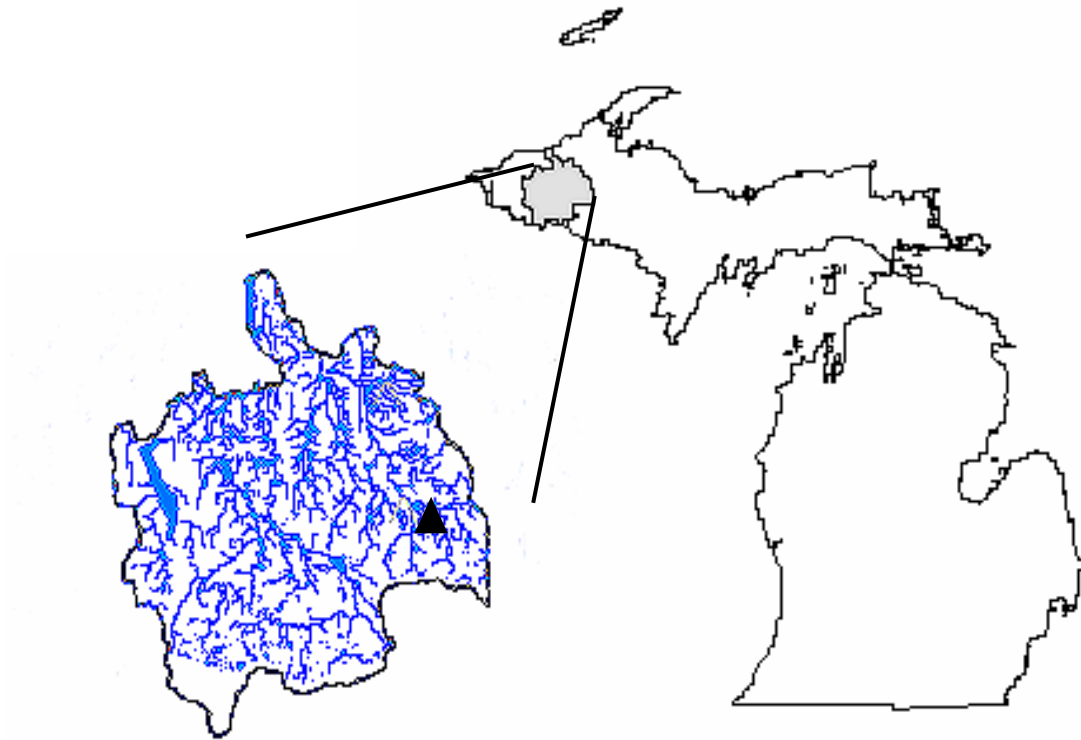


Figure 3.1. Shane Creek (▲) in the Ontonagon River watershed located in the upper peninsula of Michigan, USA.

TABLE 3.1.
 SHANE CREEK STUDY SITE CHARACTERISTICS, BASED ON
 MEASUREMENTS TAKEN IN JULY 2003. ALL MEASUREMENTS
 ARE MEANS

Characteristic	Mean
Slope (%)	0.88
Bankfull width (m)	2.8
Wetted width (m)	2.4
Depth (m)	0.12
Current velocity (m·s⁻¹)	0.14
Discharge (m³·s⁻¹)	0.046
Substrate composition (%)	
sand	36
gravel	33
pebble	17
silt	14
cobble	1
Canopy cover (%)	95
Benthic organic matter	
Quantity (g AFDM·m⁻²)	1730
Quality (C:N ratio)	44.1

3.4. Methods

3.4.1. *Colonization Experiment*

Cylindrical colonization chambers (8.5-cm diameter, 9.5-cm height; 539 cm³) were constructed of plastic mesh with closed bottoms but open tops. An outer mesh (10-mm openings) provided structure to the chambers, while an inner mesh (2-mm openings) allowed some exchange of invertebrate, BOM, and fine sediments. The inner mesh enabled chamber withdrawal from the streambed with minimal loss of contents. The open top allowed unrestricted invertebrate, BOM, and sediment exchange with the stream.

Our experiment consisted of 45 chambers. One-third of the chambers (n = 15) were filled with sterilized sand (1.1 kg = 709 mL) collected from Shane Creek but received no addition of BOM (no-BOM treatment). One-third of the chambers (n = 15) were filled with 99% sand (1.089 kg) and 1% OM (11 g) based on mass (low-BOM treatment). One-third of the chambers (n = 15) were filled with 95% sand (1.045 kg) and 5% OM (55 g) based on mass (high-BOM treatment). Treatment levels were chosen because the low-BOM treatment represents ambient conditions for 15 surveyed Upper Peninsula of Michigan streams (mean = 1.02% OM) and the high-BOM treatment is close to extreme high end of the ambient range for Shane Creek (0.07 to 6.44% OM). All sand was ashed at 550 °C for three hours. The added OM consisted of leaf litter collected from the riparian zone of Shane Creek after leaf fall and sun dried to kill litter fauna. The OM was homogenized by grinding to a consistent size (<4 mm). Stream water was added to aid in homogenizing the OM into the sand before being allocated into separate chambers.

We used a randomized complete-block design to control for any longitudinal variation in our stream reach. Five blocks of nine chambers were used, each block consisting of three replicates each of no, low, and high-BOM quantity chambers. Treatments were randomly assigned within a block. Chambers were placed 10 cm apart while blocks were spaced 2 m apart on average. Colonization chambers were buried in the stream channel with the tops flush with the streambed. One chamber of each treatment per block ($n = 5$) was randomly removed on days 4, 16, and 32. Current velocity was measured (Marsh-McBirney Flo-Mate 2000 flow meter) over each chamber before chamber removal and discharge was calculated on each sampling date (Gore 1996).

3.4.2. *BOM Processing*

BOM and invertebrates were elutriated from each core five times through nested sieves (minimum mesh size of 250 μm), which separated coarse BOM (CBOM, >1 mm) from fine BOM (FBOM, 250 μm -1 mm). A subsample of very fine BOM (VFBOM, 0.45-250 μm) was taken from the volume of water that passed through the sieves, and filtered onto a pre-ashed and weighed glass fiber filter (0.45 μm pore size). Each BOM sample was dried (48 hr at 60 $^{\circ}\text{C}$), weighed for dry mass, ashed (5 hr at 550 $^{\circ}\text{C}$), and re-weighed to determine ash-free dry mass (AFDM) (modified from Wallace et al. 1982; Wallace and Grubaugh 1996). Total BOM quantity was determined by summing all BOM size fractions. BOM quantity was reported as mass per area (e.g., Smock 1990). Inorganic substrates were dried (24 hr at 60 $^{\circ}\text{C}$) and measured for volume. Carbon and nitrogen contents of BOM were also determined (Costech Instruments® Elemental Combustion System® 4010 CHNS-O analyzer).

3.4.3. *Invertebrate Processing*

Invertebrates (>250 μm) were live-picked from the BOM and preserved in 7% formalin. A stereomicroscope under 100X magnification was used to identify invertebrates to the lowest practical taxonomic level, genus if possible, using Merritt and Cummins (1996), Hilsenhoff (1995), Pennak (1989), and Thorp and Covich (1991). Chironomidae were identified to the subfamily level. Invertebrate biomass was determined by measuring invertebrate lengths at 100X to the nearest 0.5 mm and converting lengths to biomass (DM) using length-mass regressions (Benke et al. 1999; Wallace unpublished data). Invertebrate density and biomass were computed based on the surface area of our chambers (56.7 cm^2). Invertebrate abundance and biomass were reported per area (e.g., Benke et al. 1984; Soluk 1985). Functional feeding groups (FFG) were assigned to taxa (Pennak 1989; Merritt and Cummins 1996) and apportioned by the total invertebrate abundance and biomass for each BOM treatment and collection date. Taxa richness was also determined for each chamber.

3.4.4. *Community Respiration*

Community respiration was measured for each chamber to estimate how macroinvertebrates, meiofauna, and bacteria in aggregate contributed to net oxygen consumption (e.g., Fuss and Smock 1996). Each chamber was removed from the streambed, immediately double-bagged with a known amount of stream water, and placed back in the stream to maintain ambient temperature. Dissolved oxygen and temperature were measured (Hydrolab® Surveyor® 4 sonde) at the beginning and end of 1 to 1.5-hr incubations.

3.4.5. *Statistical Analyses*

Two-way ANOVAs with randomized blocks (factors = BOM quantity, sampling date) were run on BOM quantity, invertebrate abundance and biomass, taxa richness and diversity, and community respiration over the three sampling dates. Significance was determined at $\alpha = 0.05$. On the final sampling date (day 32), we also ran one-way ANOVAs on invertebrate abundance and biomass, taxa richness, and community respiration for the different BOM quantity treatments. We reasoned that the last day of our experiment represented enough time for invertebrate colonization to stabilize (e.g., Lamberti and Resh 1985) and, therefore, results from that date would be most representative of how these variables were affected by our BOM treatments.

Simple linear regressions were used to determine whether community respiration could predict invertebrate abundance and biomass. Multiple regressions were run with C:N ratio, percent C, percent N, current velocity, and discharge as independent variables and invertebrate abundance and biomass as dependent variables.

3.5. Results

3.5.1. *Effectiveness of Treatments*

Total mean BOM quantity in our colonization chambers ranged from 136 to 3,955 g AFDM m^{-2} (0.4 to 1.6% by AFDM, Figure 3.2). The no, low, and high-BOM treatments were distinct over the three collection dates ($F_{2,108} = 59.0$, $p < 0.00001$).

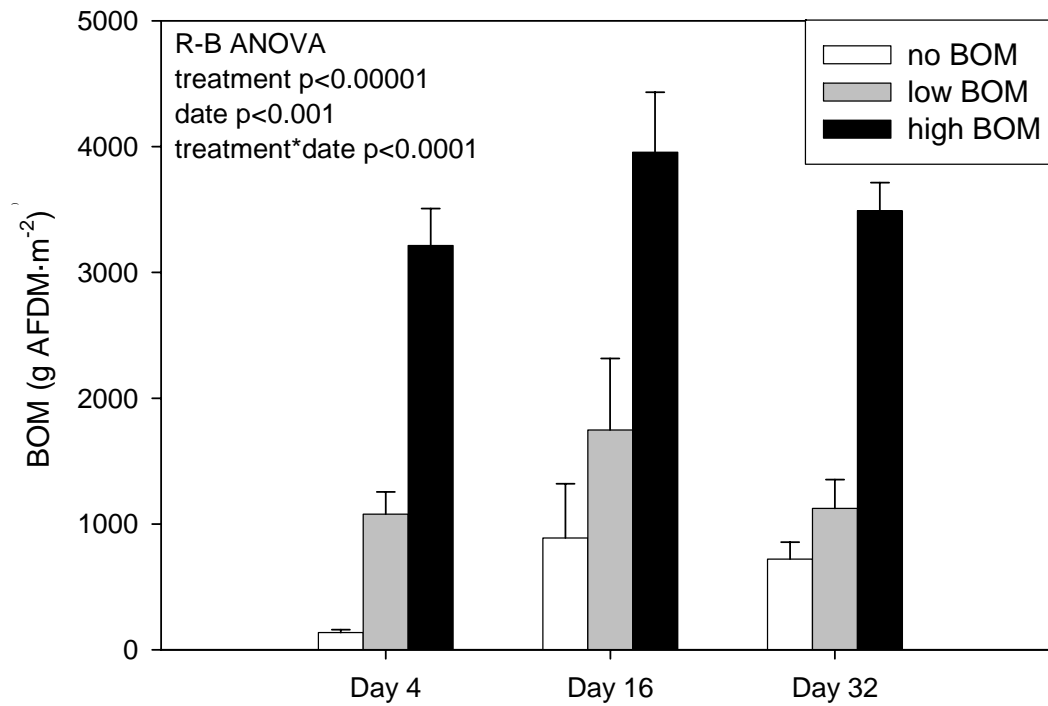


Figure 3.2. Mean total benthic organic matter (BOM) quantity (+ 1 SE; n = 5) in each BOM treatment over the three collection dates.

Proportions of BOM size fractions remained similar over all BOM treatments and collection dates. The majority of the BOM was comprised of CBOM (\bar{x} = 65.9%, SD = 5.1), followed by FBOM (\bar{x} = 20.7%, SD = 5.5), and finally VFBOM (\bar{x} = 13.3%, SD = 4.7).

3.5.2. *Invertebrate Abundance and Biomass*

Total mean invertebrate abundances in our colonization chambers ranged from 1,799 to 48,042 individuals m^{-2} (Figure 3.3). ANOVA revealed significant treatment and date effects, and a significant treatment X date interaction. Invertebrate abundance in the low-BOM treatment was generally higher than in the high-BOM treatment across all collection dates ($F_{2,108} = 3.46$, $p = 0.044$). Significantly more invertebrates were found on day 32 than on day 16 ($F_{2,108} = 4.71$, $p = 0.016$). On day 32, invertebrate abundance was significantly higher in the low-BOM treatment than in the no-BOM treatment (one-way ANOVA, $F_{2,12} = 7.46$, $p = 0.015$).

Total mean invertebrate biomass in the colonization chambers ranged from 135 to 2,680 g of dry mass m^{-2} (Figure 3.4). Invertebrate biomass did not differ significantly across BOM treatment or collection date. On day 32, invertebrate biomass was higher in the low-BOM treatment than in the no-BOM treatment (one-way ANOVA, $F_{2,12} = 8.70$, $p = 0.010$).

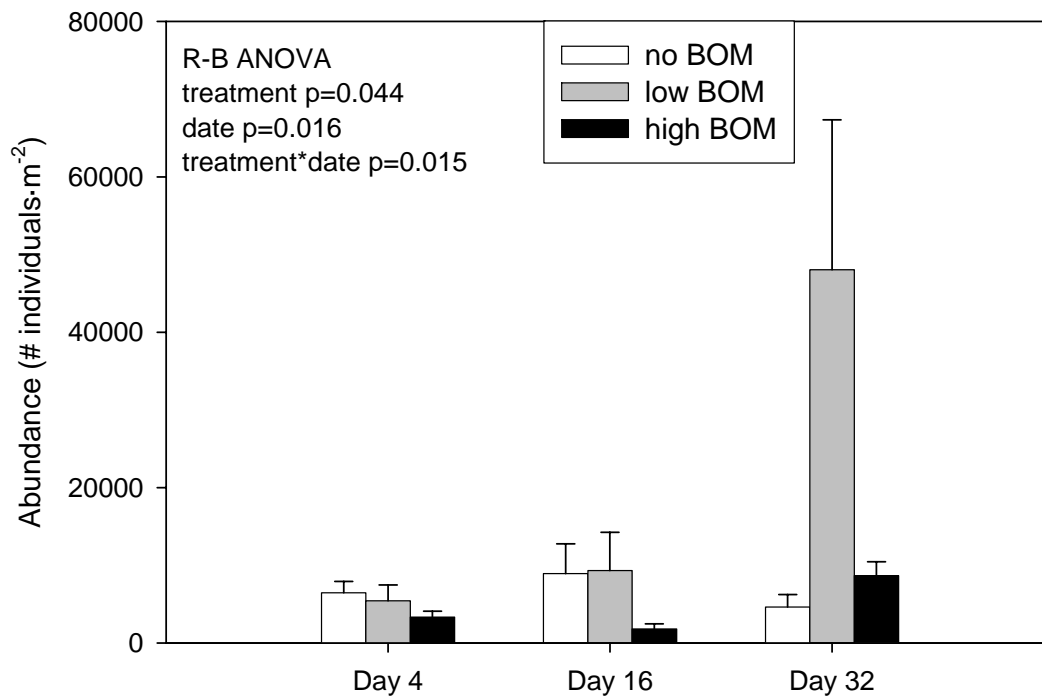


Figure 3.3. Mean invertebrate abundance (+ 1 SE; n = 5) in each BOM treatment over the three collection dates.

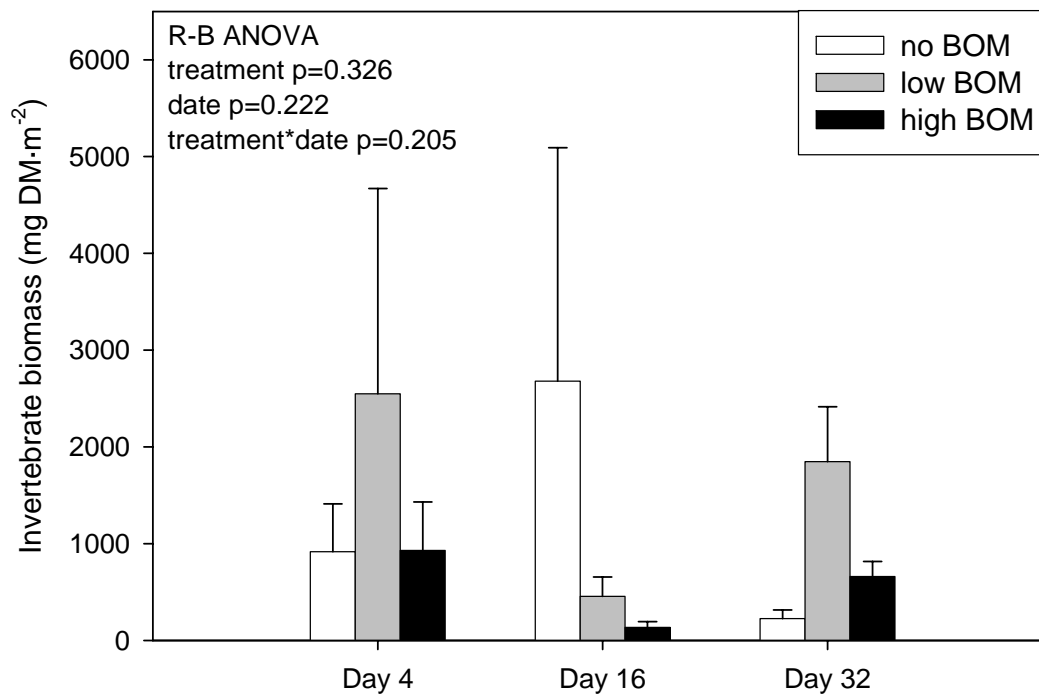


Figure 3.4. Mean invertebrate biomass (+ 1 SE; n = 5) in each BOM treatment over the three collection dates.

3.5.3. *Invertebrate Community Composition*

Functional feeding groups (see Appendix 3) were non-uniformly distributed across BOM quantity treatments and collection dates (χ^2 test, $p < 0.001$). Overall invertebrate abundance patterns during the experiment reflected the dynamics of gathering-collectors. Gathering-collectors, mostly chironomids of the subfamily Orthoclaadiinae, dominated invertebrate abundance across all treatments and collection dates ($68.6 \pm 11.1\%$; mean \pm SD; Figure 3.5). In general, predator abundance increased over time in the no and high-BOM treatments. Functional feeding group biomass varied considerably over treatments and collection dates (Figure 3.6). On day 4, shredders, mostly the caddisfly *Lepidostoma* sp., dominated the invertebrate biomass over all treatments ($82.9 \pm 4.0\%$; Figure 3.6). On days 16 and 32 of the experiment, biomass dominance shifted to predators, such as the crane fly larva *Hexatoma* sp., in the no and high-BOM treatments ($77.5 \pm 8.8\%$). In the low-BOM treatment, shredders, predators, and gathering-collectors contributed about equal biomass. Invertebrate taxa richness in the colonization chambers was variable and averaged 4 to 15 taxa per chamber (Figure 3.7). Taxa richness was higher in the low-BOM treatment than in the high-BOM treatment during the experiment ($p = 0.025$). Invertebrates of the subfamilies Chironomidae, Chironomini, Orthoclaadiinae, and Tanytarsini made up a major proportion of total invertebrate abundance and this trend appeared independent of treatment (Figure 3.8). The proportion of Chironomini abundance and biomass increased over time in all treatments. The proportion of Trichopteran abundance and biomass decreased over time in all treatments.

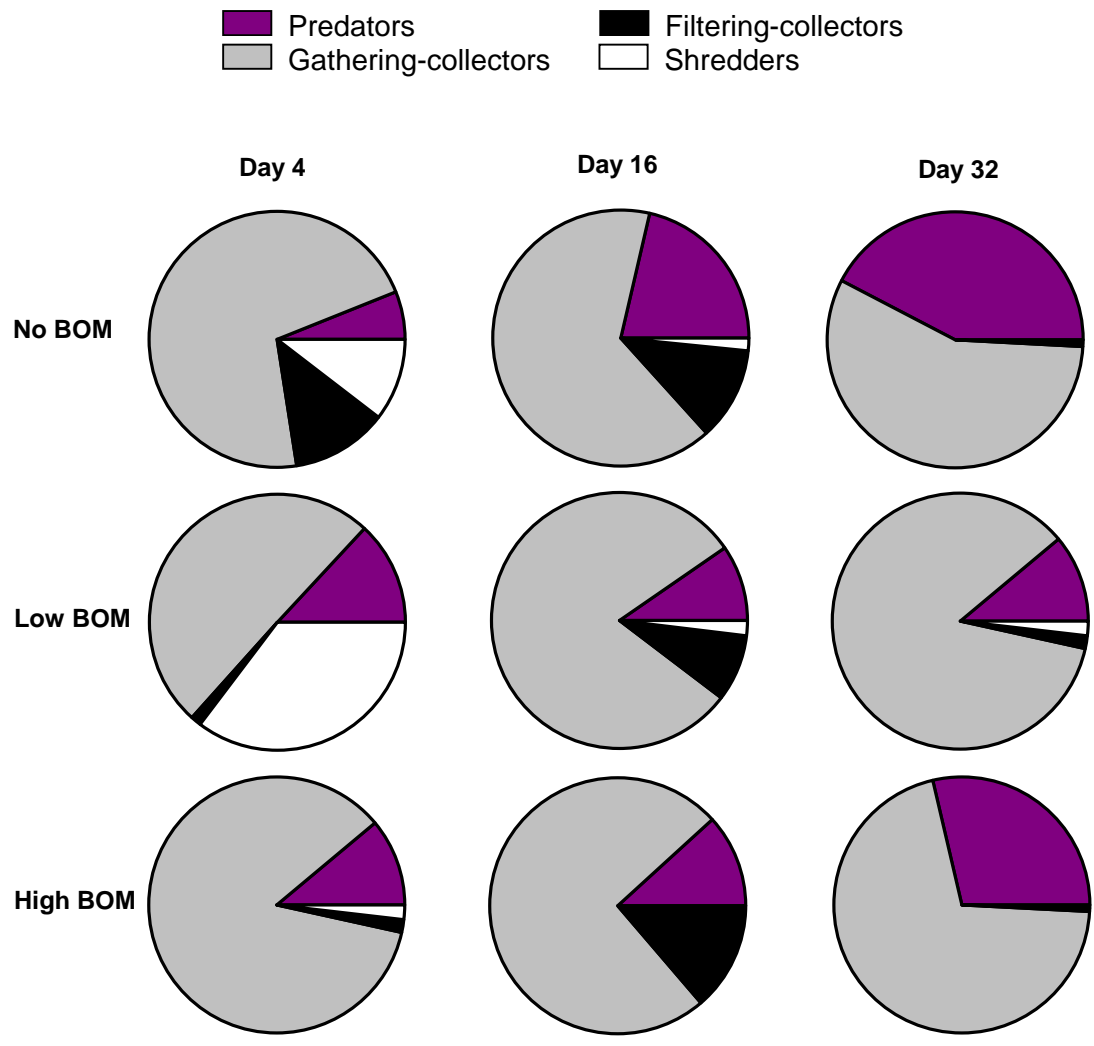


Figure 3.5. Functional feeding group proportions of total invertebrate abundance in each BOM treatment over the three collection dates.

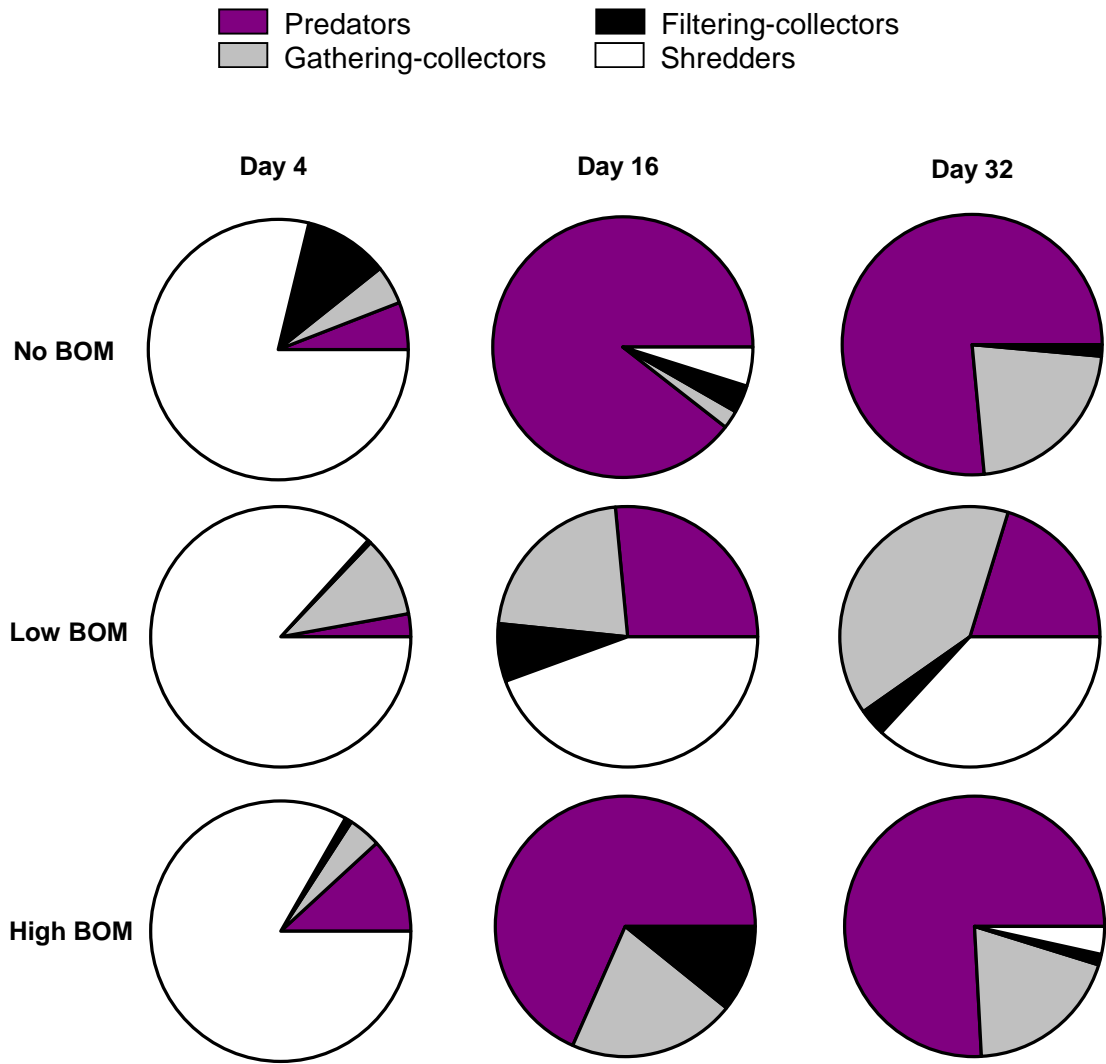


Figure 3.6. Functional feeding group proportions of total invertebrate biomass in each BOM treatment over the three collection dates.

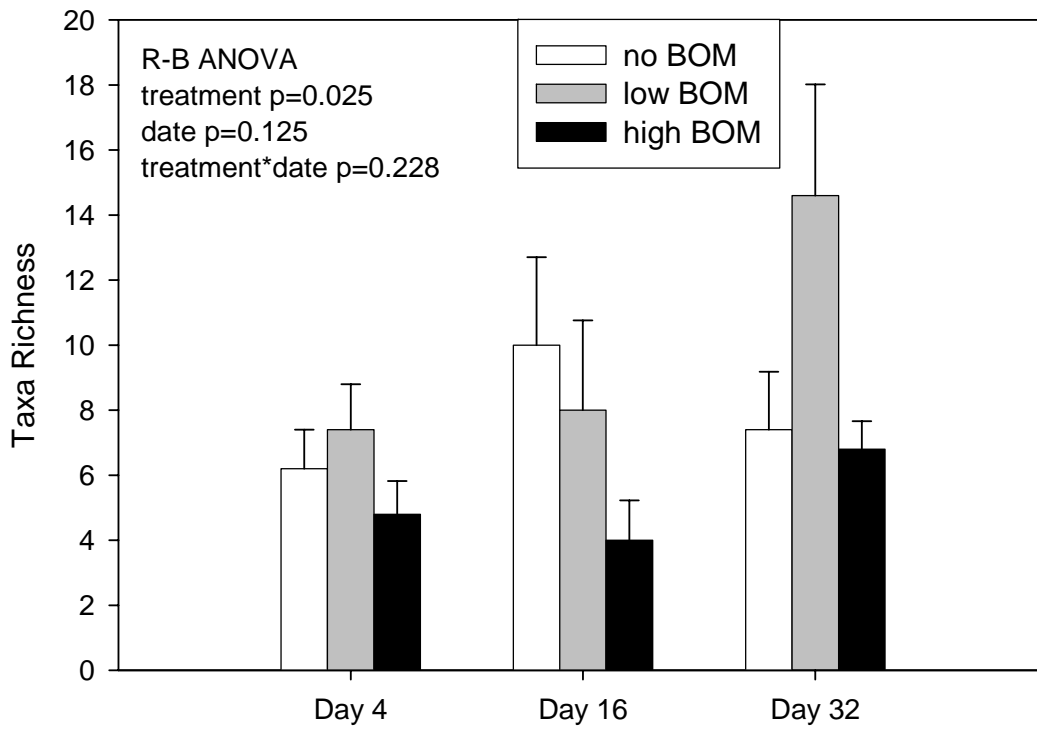


Figure 3.7. Mean taxa richness (+ 1 SE; n = 5) in each BOM treatment over the three collection dates.

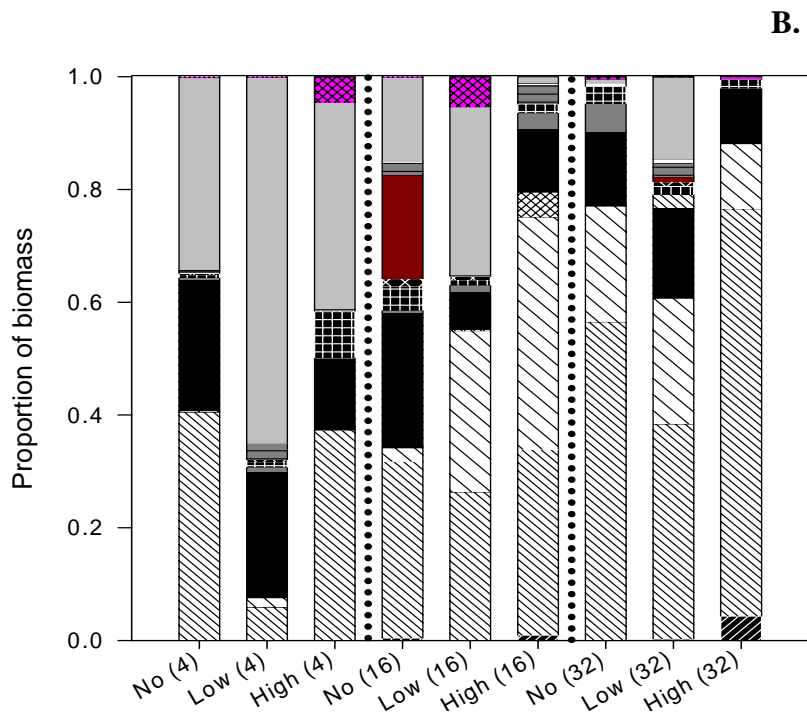
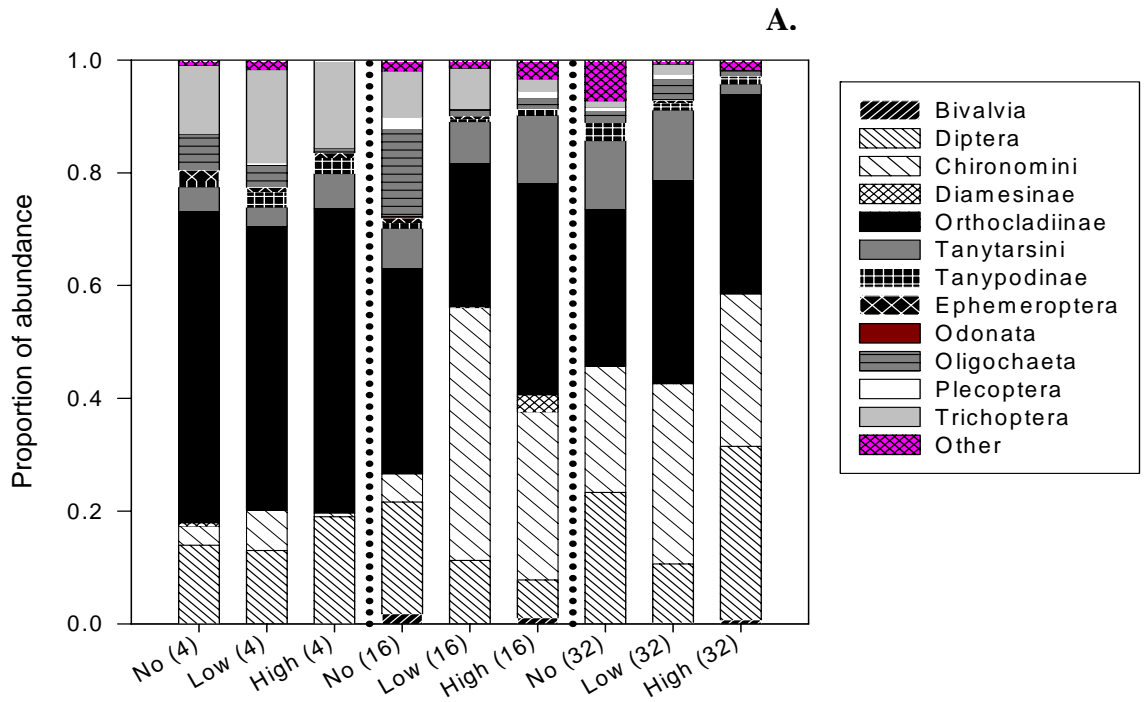


Figure 3.8. Taxa proportions of total invertebrate abundance (A) and biomass (B) in each BOM treatment over the three collection days (indicated in parentheses). ‘Diptera’ refers to all dipterans excluding the family Chironomidae. ‘Other’ refers to all invertebrates not belonging to any of the listed taxa.

3.5.4. *Community Respiration and BOM Quality*

Net community respiration was significantly higher in the high-BOM treatment than in the low-BOM treatment over the experiment ($F_{2,108} = 4.888$, $p = 0.013$; Figure 3.9). Respiration rate did not differ significantly among collection dates.

BOM quality indices (C:N ratio, percent C, and percent N) suggested that all treatments had broadly similar BOM quality, regardless of whether BOM was added (low and high-BOM treatments) or accumulated naturally over time (no-BOM treatment) (Table 3.2). C and N quantity were broadly similar within treatments regardless of collection date. Most BOM quality indices were not significantly related to either invertebrate abundance or biomass. Invertebrate biomass was negatively related to C:N ratio, but C:N ratio explained very little of the variation in biomass ($R^2 = 0.079$, $p = 0.034$).

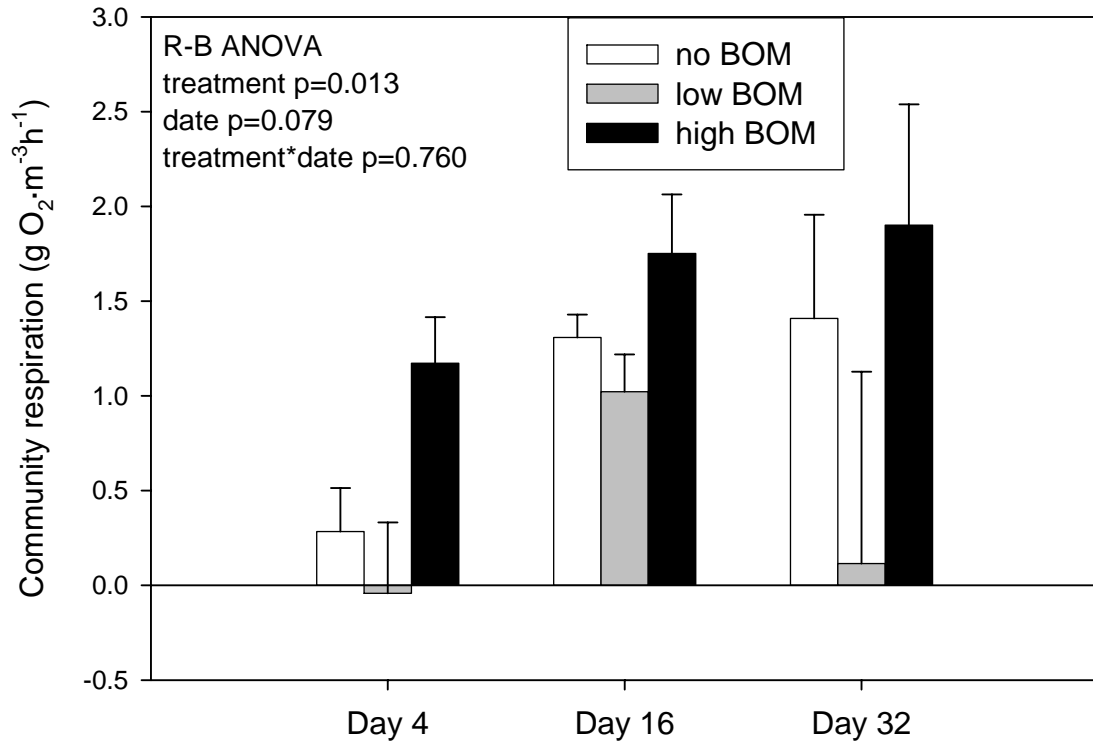


Figure 3.9. Mean net community respiration (+ 1 SE; n = 5) per volume of sediment in each BOM treatment over the three collection dates.

TABLE 3.2.

MEAN (SE; n = 3) ORGANIC MATTER QUALITY FOR EACH BOM
TREATMENT OVER ALL COLLECTION DATES

	No BOM	Low BOM	High BOM
% C	30.56 (2.16)	37.43 (0.90)	41.97 (1.13)
% N	0.87 (0.09)	0.95 (0.05)	1.09 (0.04)
C:N	41.78 (4.62)	46.46 (1.63)	45.32 (1.12)
g C AFDM·m ⁻²	194.54 (76.19)	490.45 (69.96)	1478.06 (74.83)
g N AFDM·m ⁻²	5.14 (1.95)	12.84 (2.18)	38.27 (0.93)

3.6. Discussion

BOM content of sand affected invertebrate community metrics in Shane Creek, but not in the positive linear manner that we expected. At the end of the experiment, invertebrate abundance, biomass, and taxa richness were highest in the low-BOM treatment whereas the high-BOM treatment did not differ significantly from the no-BOM treatment. This unimodal pattern contrasts with previous field experiments that found a positive linear relationship between BOM biomass and invertebrate abundance (Egglisshaw 1964; Rabeni and Minshall 1977; Culp et al. 1983). BOM quantity also affected invertebrate functional feeding group composition. Invertebrate biomass was dominated by shredders at the beginning of the experiment when added BOM was still “unprocessed”. In the middle of the experiment, biomass of gathering-collectors increased perhaps in response to increasing abundance of FBOM. At the end of the experiment, biomass dominance shifted to predators in the no and high-BOM treatments. Although predators in the low-BOM treatment followed a similar pattern of increasing biomass over time, they were not dominant at the end of the experiment. Regardless of treatment, invertebrate numbers overall were dominated by small gathering-collectors that focus on FBOM. The high numbers of midge larvae of the family Chironomidae have high turnover rates (Benke 1998) and may be able to support higher proportions of predators.

Community respiration was greater in the high-BOM treatment than in the low-BOM treatment. Bacterial and meiofaunal activity associated with BOM likely contributed to community respiration (Brunke and Fischer 1999). Community respiration differed among BOM treatments but the differences could not be explained by

macroinvertebrate abundance or biomass and therefore likely were microbially mediated. Fuss and Smock (1996) reported that benthic respiration rates were positively correlated with particulate organic matter. Brunke and Fischer (1999) found strong positive correlations between bacterial abundance and production and (1) interstitial particulate organic matter and (2) hyporheic invertebrate abundance and taxa richness. We could not distinguish among the relative contributions to respiration by macroinvertebrates, meiofauna, and bacteria, but results suggest that differences were not due solely to differences in macroinvertebrates.

BOM as a food resource appeared to influence the colonization of invertebrates in our experiment, but two additional factors, treatment differences in dissolved oxygen and a predator effect, may have modified invertebrate community responses to BOM quantity. Reduced invertebrate abundance and biomass in the high-BOM treatment relative to the low-BOM treatment may have been due to higher biological oxygen demand in chambers with higher OM content. Higher oxygen demand, measured as community respiration, in the high-BOM treatment (mean = $1.61 \text{ g O}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$) than in the low-BOM treatment (mean = $0.36 \text{ g O}_2 \cdot \text{m}^{-3} \cdot \text{h}^{-1}$) may have reduced available interstitial dissolved oxygen leading to less favorable environmental conditions for invertebrates. Predation may also have contributed to the lower invertebrate abundance and biomass observed in the no and high-BOM treatments compared to the low-BOM treatment. Functional feeding group analyses revealed increasing numbers and biomass of predators over time in the no and high-BOM treatments, but not in the low-BOM treatment. Possibly higher dissolved oxygen levels in the low-BOM treatment combined with relaxed predation may have influenced invertebrate responses to differences in BOM quantity.

BOM quality appeared to have little effect on invertebrate community responses in our experiment. However, quality (i.e., C:N ratio) of added BOM may have been too low to strongly influence invertebrate colonization in the different treatments. Mean BOM C:N ratios ranged from 41.8 to 46.5 in our experiment, whereas Findlay et al. (2002) reported C:N ratios of leaves as low as 18.2 across nine streams. Food N content is also positively correlated with assimilation efficiency for aquatic invertebrates (Pandian and Marian 1986), and N content can range up to 5% for fresh leaves (Iversen 1974). By comparison, mean %N ranged from 0.87 to 1.09 for our added BOM, suggesting low food quality. BOM quality may have been low because leaves were gathered in the early summer from the riparian zone where they had been leached since the previous autumn. Therefore, the lack of a BOM quality effect in our experiment is not surprising.

In summary, several invertebrate community metrics including invertebrate abundance, biomass, FFG composition, and taxa richness were affected by the BOM content of sand. The low-BOM treatment generally supported a more abundant and diverse invertebrate community than the no or high-BOM treatments. Lower biotic oxygen demand and relaxed predation may have accounted for greater suitability of the low-BOM treatment for invertebrates. Thus, BOM quantity may affect invertebrate colonization and distributional patterns in a non-linear manner.

3.6.1. *Concluding Remarks*

Sand habitats are common features of stream ecosystems, especially in areas with lacustrine geologies. Even though sand is considered a less suitable habitat for macroinvertebrates than coarser substrates, habitat suitability of different substrate patches may vary widely for colonizing invertebrates. Our study demonstrated that use of sand habitats by invertebrates may be due in part to BOM content, which may influence overall community metrics. Further studies of sand habitats in streams are needed to narrow the information gap between this often-dominant substrate and better-studied cobble and gravel habitats.

3.7. Acknowledgments

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3.8. Literature Cited

- Anderson, N.H., and K.W. Cummins. 1979. Influences of diet on life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36:335-342.
- Bärlocher, F. 1983. Seasonal variation of standing crop and digestibility of CPOM in a Swiss Jura stream. *Ecology* 64:1266-1272.
- Benke, A.C. 1998. Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. *Ecology* 79:899-910.
- Benke, A.C., A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308-343.
- Benke, A.C., T.C. Van Arsdall, Jr., D.M. Gillespie, and F.K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25-63.
- Brady, L., and B.C. Cowell. 2003. Colonization of fine particulate organic matter by invertebrates in a Central Florida stream. *Invertebrate Biology* 122:83-92.
- Brunke, M., and H. Fischer. 1999. Hyporheic bacteria-relationships to environmental gradients and invertebrates in a prealpine stream. *Archiv für Hydrobiologie* 146:189-217.
- Culp, J.M., S.J. Walde, and R.W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1568-1574.
- Cummins, K.W., and G.H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* 34:145-181.
- Doeg, T.J., R. Marchant, M. Douglas, and P.S. Lake. 1989. Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. *Freshwater Biology* 22:57-64.
- Egglishaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *The Journal of Animal Ecology* 33:463-476.
- Findlay, S., J. Tank, S. Dye, H.M. Valett, P.J. Mulholland, W.H. McDowell, S.L. Johnson, S.K. Hamilton, J. Edmonds, W.K. Dodds, and W.B. Bowden. 2002. A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. *Microbial Ecology* 43:55-66.

- Fuss, C.L., and L.A. Smock. 1996. Spatial and temporal variation of microbial respiration rates in a blackwater stream. *Freshwater Biology* 36:339-349.
- Gore, J.A. 1979. Patterns of initial benthic recolonization of a reclaimed coal strip-mined river channel. *Canadian Journal of Zoology* 57:2429-2439.
- Gore, J.A. 1982. Benthic invertebrate colonization: source distance effects on community composition. *Hydrobiologia* 94:183-193.
- Gore, J.A. 1996. Discharge Measurements and streamflow analysis pp. 53-74 in Hauer, F.R. and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego.
- Haines, T.A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. *Transactions of the American Fisheries Society* 110:669-707.
- Hall, R.O., G.E. Likens, and H.M. Malcom. 2001. Trophic basis of invertebrate production in 2 streams at Hubbard Brook Experimental Forest. *Journal of the North American Benthological Society* 20:432-447.
- Hall, R.O., J.B. Wallace, and S.L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81:3445-3463.
- Hauer, F.R., and G.A. Lamberti (eds.). 1996. *Methods in stream ecology*. Academic Press, San Diego.
- Heinrich, E.W. 2001. Economic geology of the sand and sandstone resources of Michigan. Michigan Department of Environmental Quality Geological Survey Division. Report of Investigation 21. Lansing, MI 48909.
- Hilsenhoff, W.L. 1995. Aquatic insects of Wisconsin. Keys to Wisconsin genera and notes on biology, habitat, distribution, and species. University of Wisconsin Natural History Museums Council Pub. Coop. Ext. Publications #G3648, Room 245, 30 N. Murray St., Madison, WI 53715.
- Iversen, T.M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos* 25:278-282.
- Lamberti, G.A., and V.H. Resh. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macroinvertebrates. *Freshwater Biology* 15:21-30.
- Merritt, R.W., and K.W. Cummins (eds.). 1996. *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt, Dubuque, IA.

- Metzler, G.M., and L.A. Smock. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47:588-594.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. Pages 358-400 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Miyake, Y., and S. Nakano. 2002. Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology* 47:219-230.
- Müller, K. 1982. The colonization cycle of freshwater insects. *Oecologia* 52:202-207.
- Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. Pages 323-357 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Ottawa National Forest. 1986. Plan Appendix D: Ecological classification system description. Land and Resources Management Plan.
- Palmer, M.A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *Journal of the North American Benthological Society* 9:17-25.
- Pandian, T.J., and M. P. Marian. 1986. An indirect procedure for the estimation of assimilation efficiency of aquatic insects. *Freshwater Biology* 16:93-98.
- Peckarsky, B.L. 1980. Influence of detritus upon colonization of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 37:957-963.
- Peckarsky, B.L. 1984. Predator-prey interactions among aquatic insects. Pages 196-254 *in* Resh, V.H., and D.M. Rosenberg (eds.). *The ecology of aquatic insects*. Praeger, New York.
- Pennak, R.W. 1989. *Freshwater invertebrates of the United States*, 3rd ed. Wiley, New York.
- Rabeni, C.F., and G.W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Resh, V.H., and D.M. Rosenberg (eds.). 1984. *The ecology of aquatic insects*. Praeger, New York.
- Robertson, A.L. 2000. Lotic meiofaunal community dynamics: colonization, resilience and persistence in a spatially and temporally heterogeneous environment. *Freshwater Biology* 44:135-147.

- Rowe, L., and J.S. Richardson. 2001. Community responses to experimental food depletion: resource tracking by stream invertebrates. *Oecologia* 129:473-480.
- Smock, L.A. 1990. Spatial and temporal variation in organic matter storage in low-gradient, headwater streams. *Archiv für Hydrobiologie* 118:169-184.
- Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys, 2nd ed. United States Department of Agriculture, Washington, D.C.
- Soluk, D.A. 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1296-1302.
- Thorp, J.H., and A.P. Covich (eds.). 2001. Ecology and classification of North American freshwater invertebrates, 2nd ed. Academic Press, San Diego, CA.
- Tillman, D.C., A.H. Moerke, C.L. Ziehl, and G.A. Lamberti. 2003. Subsurface hydrology and degree of burial affect mass loss and invertebrate colonization of leaves in a woodland stream. *Freshwater Biology* 48:98-107.
- Vannote, R.L., and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* 115:667-695.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409-442.
- Wallace, J.B., and J.W. Grubaugh. 1996. Transport and storage of FPOM pp. 191-215 *in* Hauer, F.R. and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego.
- Wallace, J.B., D.H. Ross, and J.L. Meyer. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. *Ecology* 63:824-838.
- Williams, D.D., and H.B.N. Hynes. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology* 4:233-256.
- Williams, D.D., and H.B.N. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27:265-272.
- Williams, D.D., and J.H. Mundie. 1978. Substrate size selection by stream invertebrates and the influence of sand. *Limnology and Oceanography* 23:1030-1033.

CHAPTER 4

SYNTHESIS AND CONCLUSIONS

4.1. Summary of Results

My study of 15 streams within three watersheds of the ONF (Chapter 2) demonstrated that BOM quantity and invertebrate community metrics in sand habitats differed among watersheds. Streams in the Black-Presque Isle Rivers watershed had higher proportions of very fine BOM (VFBOM) and lower proportions of coarse BOM (CBOM) than streams in the Ontonagon River or Sturgeon River watersheds. These proportional differences in BOM size fractions may be related to increased retention and accumulation of VFBOM compared to CBOM in the coarser substrates in the Black-Presque Isle Rivers watershed (D_{50} = pebble) than in the finer substrates in the Ontonagon River and Sturgeon River watersheds (D_{50} = sand). In contrast, streams in the Sturgeon River watershed had higher invertebrate biomass and mean individual size than streams in the Black-Presque Isle Rivers or Ontonagon River watersheds. This difference was driven by the presence of a few large invertebrates.

This study also demonstrated that invertebrate functional feeding groups were similar among all streams. Invertebrate abundance and biomass in sand habitats overall were dominated by gathering-collectors. The major proportion of the invertebrates were

made up of Chironomid midge larvae, which are small, worm-like, burrowing invertebrates that are adapted to living in sand habitats and have high growth rates and rapid turnover (Palmer and Strayer 1996; Wallace and Anderson 1996; Boulton 2000). In contrast to studies in coarser substrates (Egglisshaw 1964; Rabeni and Minshall 1977; Culp et al. 1983; Drake 1984; Wallace et al. 1999), BOM quantity or quality had little apparent effect on invertebrate community metrics in sand habitats of our study streams.

The 32-day colonization experiment conducted in Shane Creek (Chapter 3) demonstrated that the BOM content of sand affected some invertebrate community metrics, but not in a positive linear manner as predicted. At the end of our experiment, invertebrate abundance and biomass were higher in the low-BOM treatment than the no-BOM treatment. The high-BOM treatment was not significantly different from the no-BOM treatment. Higher oxygen consumption in the high-BOM treatment than in the low-BOM treatment may have reduced interstitial dissolved oxygen, thereby leading to less favorable conditions for invertebrates. This possibility is supported by higher respiration rates (i.e., oxygen consumption) in the high-BOM treatment. BOM quantity appeared to also affect invertebrate functional feeding group composition. As in the 15-stream study, invertebrates were dominated by gathering-collectors at the end of the experiment. At the beginning of the experiment, however, invertebrate biomass was dominated by shredders, while predators increased in abundance over time. Abundant predators in the no- and high-BOM treatments, relative to the low-BOM treatment, may have contributed to reduced invertebrate numbers in those treatments by the end of the experiment (Figure 4.1).

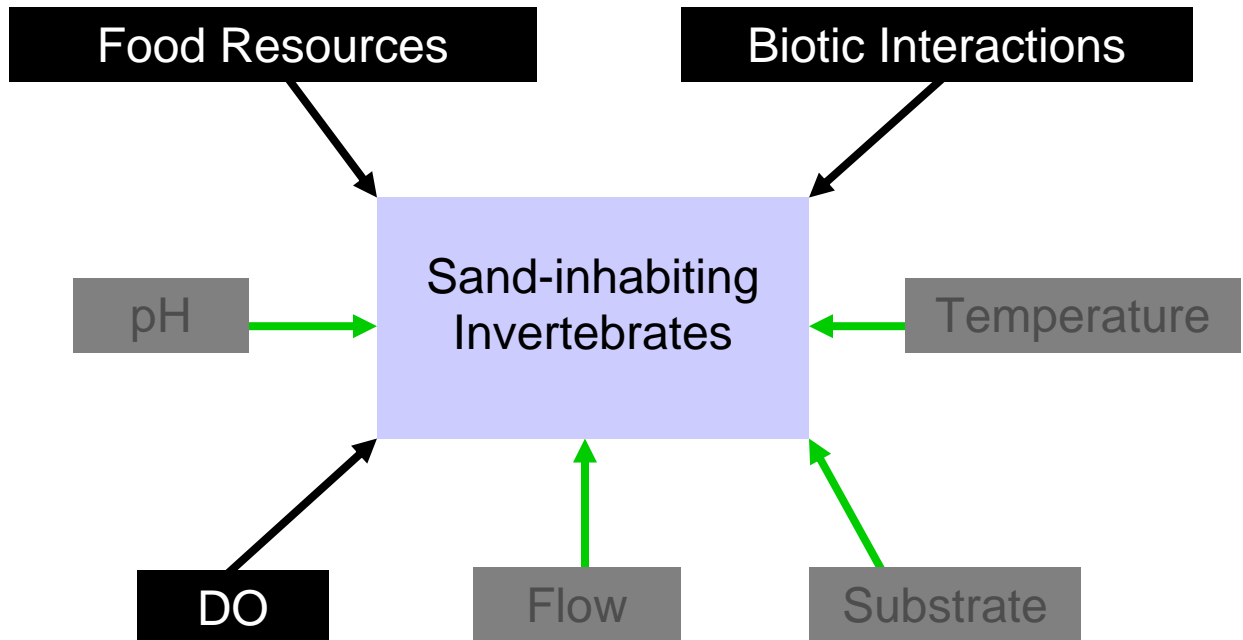


Figure 4.1. Simplified conceptual diagram of factors that may influence the distribution of stream benthic invertebrates in sand habitats. This thesis suggests that the factors in black boxes may have greater relative effects on habitat suitability in sand habitats. DO=dissolved oxygen.

4.2. Future Research Needs

In general, more studies of sand habitats in streams are necessary to elucidate the importance of this common but little-studied substrate to stream ecosystem structure and function. Our knowledge of BOM and invertebrate communities in sand habitats of streams should be improved because invertebrate community metrics in sand habitats appear to vary substantially within streams, among streams, and across watersheds. Future studies of invertebrate communities in sand habitats should strive to measure invertebrate secondary production because sand-dwelling invertebrates are often small and likely have rapid turnover (Benke et al. 1984). Production measurements will more accurately estimate the contribution of sand invertebrates to overall stream productivity. Invertebrates smaller than 250 μm were not measured during this study. However, meiofauna (e.g., rotifers, copepods, ostracods) may represent a substantial portion of the sand-dwelling community (Palmer 1990; Tillman 2003) and should be examined in future studies. Finally, additional research is needed on the environmental factors potentially important in determining the community structure of sand-dwelling invertebrates. For example, dissolved oxygen levels may be lower in sand habitats than in coarser substrates due to limited interstitial pore space (Allan 1995). Predation and other biotic interactions may reduce numbers of otherwise abundant gathering-collectors.

4.3. Conclusions

Sand habitats are common features of stream ecosystems, especially in low-gradient areas with sandy geology. Even though sand is considered a less preferred habitat for macroinvertebrates than coarser substrates, habitat suitability of different substrate patches may vary widely among invertebrates. The majority of sand-dwelling invertebrates in our study were gathering-collectors of the family Chironomidae. Our study demonstrated that BOM and invertebrate community metrics in sand habitats differ within streams, among streams, and across watersheds. While our observational studies showed that BOM quantity had little effect on invertebrate community metrics in sand habitats of surveyed streams, our field experiment suggested that use of sand habitats by invertebrates may be related in part to BOM content, which may influence overall community metrics. Further studies of sand habitats in streams are needed to narrow the information gap between this often-dominant substrate and better-studied cobble and gravel habitats of stream ecosystems.

4.4. Literature Cited

- Allan, J.D. 1995. Stream ecology: structure and function of running waters. Kluwer Academic Publishers, Boston.
- Benke, A.C., T.C. Van Arsdall, Jr., D.M. Gillespie, and F.K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs* 54:25-63.
- Boulton, A. 2000. The subsurface macrofauna. Pages 337-361 *in* Jones, J.B., and P.J. Mulholland (eds.). *Streams and ground waters*. Academic Press, San Diego, CA.
- Culp, J.M., S.J. Walde, and R.W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1568-1574.
- Drake, J.A. 1984. Species aggregation: the influence of detritus in a benthic invertebrate community. *Hydrobiologia* 112:109-115.
- Egglshaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *The Journal of Animal Ecology* 33:463-476.
- Palmer, M.A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *Journal of the North American Benthological Society* 9:17-25.
- Palmer, M.A., and D.L. Strayer. 1996. Meiofauna. Pages 315-337 *in* Hauer, F.R., and G.A. Lamberti (eds.). *Methods in stream ecology*. Academic Press, San Diego, CA.
- Rabeni, C.F., and G.W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Tillman, D.C., A.H. Moerke, C.L. Ziehl, and G.A. Lamberti. 2003. Subsurface hydrology and degree of burial affect mass loss and invertebrate colonization of leaves in a woodland stream. *Freshwater Biology* 48:98-107.
- Wallace, J.B., and N.H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 *in* Merritt, R.W., and K.W. Cummins (eds.). *An introduction to the aquatic insects of North America*, 3rd ed. Kendall/Hunt Publishing Company, Dubuque, IA.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409-442.

APPENDIX 1.

FUNCTIONAL FEEDING GROUP ASSIGNMENTS FOR BENTHIC INVERTEBRATES (ORDER, FAMILY, GENUS) FROM 15 STREAMS IN THE BLACK-PRESQUE ISLE RIVERS, ONTONAGON RIVER, AND STURGEON RIVER WATERSHEDS BASED ON MERRITT AND CUMMINS (1996) AND PENNAK (1989). GC = GATHERING-COLLECTOR, FC = FILTERING COLLECTOR, P = PREDATOR, PH = PIERCING-HERBIVORE, S = SHREDDER. (*** VERY COMMON, ** FREQUENT, * RARE)

Taxon	FFG	Stream														
		EBPI	MON	NAR	REE	JUG	LEV	MCG	ST	SHA	TM (1)	TM (2)	WAL	PER	SIL	WBS
Bivalvia	FC		**		*		*	**	*	*	*		*	*		*
Coleoptera																
Elmidae <i>Stenelmis</i>	GC		*	*												
Diptera																
Ceratopogonidae <i>Bezzia</i>	P								*		*					*
Ceratopogonidae <i>Probezzia</i>	P	*	*	*	*	*		*	*	*	**	*	*	*		*
Chironomidae Chironomini	GC	***	***	*	**	**	**	***	*	*	**	***	*	***	**	***
Chironomidae Diamesinae	GC		*		*	*						*				
Chironomidae Orthoclaadiinae	GC	*	*	**	***	**	***	**	**	***	*	**	**	**	*	*
Chironomidae Prodiamesinae	GC					*	**	*	**	*			*	*		
Chironomidae Tanypodinae	P	*	***	*	*	*	**	*	*	*	**	*	*	*		**
Chironomidae Tanytarsini	GC	***	**	*	**	*	**	***	*	*	***	***	***	***	*	**
Tabanidae <i>Chrysops</i>	P	*				*	*	*								
Tipulidae <i>Dicranota</i>	P				*	*			*	*			*			
Tipulidae <i>Hexatoma</i>	P		*	*		*	*	*	*	*	*	*	*		*	
Tipulidae <i>Tipula</i>	S					*			*	*			*			
Ephemeroptera																
Ameletidae <i>Ameletus</i>	GC						*				*	*		*		*
Baetidae <i>Baetis</i>	GC				*		*					*	*		*	
Caenidae <i>Brachycercus</i>	GC							*				*				
Ephemerellidae <i>Serratella</i>	GC												*			
Heptageniidae <i>Stenacron</i>	GC									*						
Leptophlebiidae <i>Paraleptophlebia</i>	GC	*	**	*	*		*				*					

APPENDIX 1.

CONTINUED

Taxon	FFG	Stream														
		EBPI	MON	NAR	REE	JUG	LEV	MCG	ST	SHA	TM (1)	TM (2)	WAL	PER	SIL	WBS
Hemiptera																
Corixidae	PH													*		
Gerridae <i>Rheumatobates</i>	P														*	
Megaloptera																
Sialidae <i>Sialis</i>	P													*		
Odonata																
Cordulegastridae <i>Cordulegaster</i>	P		*		*			*					*			
Gomphidae <i>Gomphurus</i>	P													*		
Oligochaeta	GC	**	*	**	***		*	*	*	*	**	**	*	*		**
Plecoptera																
Chloroperlidae <i>Haploperla</i>	P		**	**	**					*						
Trichoptera																
Philopotamidae <i>Dolophilodes</i>	FC											*				
Hydroptilidae <i>Hydroptila</i>	PH	*														
Lepidostomatidae <i>Lepidostoma</i>	S						*						*			
Leptoceridae <i>Oecetis</i>	P															*

APPENDIX 2.

MEAN (S.E.) PERCENTAGE OF TOTAL INVERTEBRATE
ASSEMBLAGE REPRESENTED BY CHIRONOMIDAE IN SAND
HABITATS FOR 15 STREAMS IN THE UPPER PENINSULA, MI

Stream*	% Abundance	% Biomass	n
EBPI	85.8 (8.5)	65.3 (31.7)	5
MON	61.3 (17.7)	43.1 (34.9)	5
NAR	37.7 (5.4)	44.8 (24.3)	5
REE	51.6 (19.5)	30.1 (15.8)	5
JUG	84.0 (11.7)	54.7 (44.3)	4
LEV	88.4 (8.1)	75.6 (21.3)	5
MCG	86.5 (8.8)	36.3 (35.8)	5
ST	57.7 (25.2)	49.4 (25.6)	10
SHA	78.0 (16.9)	54.8 (27.7)	10
TM (1)	81.3 (15.2)	84.6 (10.6)	5
TM (2)	82.3 (6.8)	68.6 (19.9)	5
WAL	84.2 (13.0)	58.5 (28.0)	9
PER	78.8 (8.1)	39.0 (43.5)	5
SIL	82.9 (10.7)	95.9 (4.8)	5
WBS	63.2 (24.4)	41.6 (34.3)	5

*EBPI = East Branch Presque Isle, MON = Montowibo, NAR = Narrows, REE = Reed, JUG = Jug, LEV = Leveque, MCG = McGinty, ST = State, SHA = Shane, TM (1) = Two-Mile (1), TM (2) = Two-Mile (2), WAL = Walton, PER = Perch, SIL = Silver, WBS = West Branch Sturgeon Tributary

APPENDIX 3.

FUNCTIONAL FEEDING GROUP CLASSIFICATIONS FOR BENTHIC INVERTEBRATE TAXA COLLECTED IN SHANE CREEK, MI, BASED ON MERRITT AND CUMMINS (1996), HILSENHOFF (1995), PENNAK (1989), AND THORP AND COVICH (1991). P = PREDATOR, GC = GATHERING-COLLECTOR, FC = FILTERING-COLLECTOR, S = SHREDDER

Taxon	FFG
Bivalvia	FC
Diptera	
Athericidae <i>Atherix</i> sp.	P
Ceratopogonidae <i>Bezzia</i>	P
Ceratopogonidae <i>Probezzia</i>	P
Chironomidae Chironomini	GC
Chironomidae Diamesinae	GC
Chironomidae Orthoclaadiinae	GC
Chironomidae Prodiamesinae	GC
Chironomidae Tanypodinae	P
Chironomidae Tanytarsini	GC
Simuliidae <i>Prosimulium</i>	FC
Simuliidae <i>Simulium</i>	FC
Tabanidae <i>Chrysops</i>	P
Tipulidae <i>Dicranota</i>	P
Tipulidae <i>Hexatoma</i>	P
Tipulidae <i>Tipula</i>	S
Ephemeroptera	
Baetidae <i>Baetis</i>	GC
Ephemerellidae <i>Eurylophella</i>	GC
Ephemerellidae <i>Serratella</i>	GC
Heptageniidae <i>Stenacron</i>	GC
Leptophlebiidae <i>Paraleptophlebia</i>	GC
Megaloptera	
Sialidae <i>Sialis</i>	P
Odonata	
Cordulegastridae <i>Cordulegaster</i>	P
Oligochaeta	GC
Plecoptera	
Chloroperlidae <i>Haploperla</i>	P
Leuctridae <i>Leuctra</i>	S
Nemouridae <i>Amphinemura</i>	S
Perlodidae	P
Trichoptera	
Brachycentridae <i>Brachycentrus</i>	FC
Philopotamidae <i>Dolophilodes</i>	FC
Hydroptilidae <i>Agraylea</i>	GC
Lepidostomatidae <i>Lepidostoma</i>	S
Leptoceridae <i>Oecetis</i>	P

