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Leaf and Wood Utilization in the Middle Missouri River

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LEAF AND WOOD UTILIZATION IN THE MIDDLE MISSOURI RIVER

by

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LEAF AND WOOD UTILIZATION IN THE MIDDLE MISSOURI RIVER

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Abstract. Inputs of terrestrial plant material typically serve a vital role in food webs of lotic systems. These inputs have decreased in the Missouri River after a century of river channelization and development. Addition of organic material (e.g., leaf litter) to the river has been suggested as a means to increase fish production, through increases in secondary production at lower trophic levels.

Two experiments were conducted to test the efficacy of this approach. A microcosm study of the decomposition of cottonwood leaves (*Populus deltoides*) was conducted under controlled laboratory conditions to examine: 1) the impacts on water quality [total nitrogen (TN), total phosphorus, dissolved oxygen, pH, and dissolved organic carbon (DOC)], and 2) macroinvertebrate roles in organic matter processing. Leaf mass loss, measures of breakdown products, and macroinvertebrate gut contents indicated that invertebrates did not contribute significantly to organic matter breakdown. DOC increased significantly as a result of leaching, and TN decreased likely due to an increase in microbial biomass.

Second, natural and artificial leaves and wood were placed at two Missouri River sites to assess macroinvertebrate utilization. Disturbance due to fluctuations in discharge was the major determinant of invertebrate composition. Invertebrate abundance and diversity was also influenced by field site, material accumulated from drift, and burial (sedimentation). Wood supported a greater abundance and diversity of food and habitat resources. Biofilm and drift organic matter were the dominant materials consumed. The most abundant invertebrates (chironomids, zooplankton, oligochaetes, and trichopterans) belonged to the collector functional

feeding group, which ingest material from substrate surfaces or the water column.

Macroinvertebrate utilization of leaves and wood in the Missouri River was habitat-structure based rather than a direct food source. Leaf and wood additions to the Missouri River would likely increase DOC, which serves as a food resource for macroinvertebrates and microbes. Wood additions should have a greater impact on secondary production; however, disturbance would continue to play a dominant role.

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Table of Contents

List of Figures (FFG = Functional Feeding Group)

CHAPTER 1

CHAPTER 2

List of Tables

CHAPTER 1

CHAPTER 2

Introduction

Our dependence on the Missouri River led to a major restructuring by federal engineers, beginning in 1838 (Hesse et al. 1993). Efforts such as desnagging, channelization, and the construction of six dams have contributed to a dramatic alteration of the river ecosystem. These manipulations have contributed to a decrease in organic matter and its transport, which is thought to have contributed to an overall decrease in secondary production. In addition, and possibly of equal importance, the removal of millions of large trees from the main channel and bankline of the Missouri River in the mid-1800s (Hesse and Schmulbach 1991) has greatly contributed to loss of organic matter input. A study conducted on the only remaining unchannelized reach downstream of the dams suggested a decrease in secondary production by 61% from 1963 to 1980. Concomitant reduction of aquatic insects has contributed to the subsequent decline of fish abundance (Mestl and Hesse 1993), which has declined to less than 20% of what originally inhabited the Missouri River (Hesse and Schmulbach 1991).

The macroinvertebrate community, which is involved in detrital processing, can be divided into general functional feeding groups: (1) shredders that utilize coarse particulate organic matter (CPOM) > 1 mm, such as leaf litter from the riparian zone and macrophytes, (2) collectors that filter from the water or gather fine particulate organic matter (FPOM) > 0.45 μm to 1 mm from the sediments, and (3) grazers and scrapers that primarily shear attached algae from surfaces (Vannote et al. 1980). The link between detritus and invertebrates is important in stream ecosystems. Inputs of terrestrial plant material contribute 50-99% of the energy processed in stream communities (Fisher and Likens 1973). When detritus such as a dead leaf enters the stream, it rapidly leaches most of its soluble substances (Kaushik and Hynes 1971). Microbes then colonize the leaf and convert complex compounds of leaf material into subunits that invertebrates can more easily digest

(Kaushik and Hynes 1971, Barlocher and Kendrik 1975, Rong 1993). Finally, energy is transferred to higher trophic levels through predation by fish on the invertebrates.

The role of terrestrially derived CPOM in large rivers is not well understood. The general model derived from previous studies is that leaf litter is decomposed by microbes and shredding macroinvertebrates (Hill et al. 1992). Examinations of leaf breakdown suggest that the invertebrate fauna have an important influence on leaf breakdown rates (Hart and Howmiller 1975, Iversen 1975, Sedell et al. 1975, Kirby et al. 1983) and that shredders significantly increase these rates (Peterson and Cummins 1974, Kirby et al. 1983). Here the microbes convert the material to a more palatable and nutritious food source for the invertebrates, and the invertebrates feed on both microbes and leaf material (Fig. 1a). Invertebrates accelerate the rate of decomposition by shredding and exposing new surfaces to microbial degradation. However, it has been shown that in streams of the southern Great Plains, shredder densities are extremely low and yet leaf litter processing is rapid (Short et al. 1984, Smith 1986, Tate and Gurtz 1986, Hill et al. 1988, Hill et al. 1992). Microbial processing may be the most important biotic agent of decay in prairie streams, with invertebrates not acting as shredders, but still feeding on microbes and therefore maintaining only an indirect link with the leaves themselves (Fig. 1b). Two studies from the southern Great Plains on 2nd to 4th order streams support this contention (Short et al. 1984, Hill et al. 1992). Therefore, the question is whether invertebrates of the Missouri River would utilize introduced leaf material as a food source, or if this material serves as a structural habitat for invertebrates, providing stability and alternative food resources.

These conflicting hypotheses on the role of macroinvertebrates in leaf decomposition are interesting because of their implications for the structure and function of lotic systems and the influence of geomorphic features of the region encompassing the river. This is also important from a managerial point of view. Hesse and Sheets (1993) state that leaves and trees may be added to

the river to temporarily replace the organic matter and nutrients lost due to impoundment. In an attempt to increase fish biomass in the Missouri River, the Nebraska Game and Parks Commission has considered a plan to stimulate secondary production within the river, by adding detritus in the form of terrestrial plant material. The plan assumes that restoration of CPOM and FPOM concentrations to historically higher levels will stimulate secondary production, which will, in turn, provide more food for fish. Two conducted experiments test these assumptions.

The overall research goal was to understand the role of terrestrial plant material (CPOM) in the Missouri River ecosystem, thus facilitating scientifically based management decisions regarding organic matter additions. The aims of this project were to answer the following questions: 1) How do macroinvertebrates utilize terrestrial organic material in the Missouri River? 2) Will common invertebrates contribute significantly to organic matter processing beyond that of the microbes? 3) Which of the existing river models best describes the structure and function of Missouri River communities? The specific objectives were to: (1) compare macroinvertebrate and microbial breakdown of leaves both in the field and in laboratory microcosms, (2) assess associated impacts of leaf breakdown on water quality, and (3) determine whether invertebrate use of terrestrial plant material is nutritionally or habitat-structure based. Two experiments were conducted: a laboratory experiment to observe microbial and macroinvertebrate decomposition of cottonwood leaves, and a field experiment to examine the basis of macroinvertebrate utilization of leaf and wood material.

CHAPTER 1

A microcosm study of the decomposition of cottonwood leaves: impacts on water quality and macroinvertebrate contributions

This lab experiment addressed the questions: 1) what effects leaf addition may have on water quality in the Missouri River, and 2) whether macroinvertebrates make a significant contribution to organic matter processing in the Missouri River. A pilot study was also conducted to ensure that water temperature, light intensity, current velocity, initial pH, and initial dissolved oxygen mimicked summer conditions at field sites where terrestrial organic matter addition has been proposed.

Artificial streams are useful since they allow for close observation and control over environmental conditions, species pools, and emigration/immigration (Frissell and Lonzarich 1996). In addition, replicates and a wide variety of experimental manipulations are possible (Frissell and Lonzarich 1996).

Microcosms have gained much attention in aquatic ecotoxicology studies, and have proven successful in predicting "approximate responses in natural situations" (Joern and Hoagland 1996). Various authors have emphasized a need for whole community studies and the advantages microcosms have to offer. Taub (1997) emphasized the importance of multispecies lab studies using microcosms and cites advantages of "statistical power, speed of analyses, demonstrated reproducibility among laboratories, modest expense (compared to field studies)" and the potential extraction of parent and transformation products.

In this study, we applied this approach to the study of nutrient dynamics, to predict the impacts of cottonwood leaf addition on a Missouri River community. However, it is important to realize that substantial realism may be lost since elements and processes important in natural systems may be left out or severely simplified (Frissell and Lonzarich 1996).

1.1. Materials and Methods

1.1.1. *Artificial Streams*

Sixteen recirculating, artificial streams in the University of Nebraska aquatic microcosm research facility, each constructed of a 114-L oval run with a central divider, were arranged in two parallel rows of eight. Each stream was circulated by an electric variable-speed motor with paddle wheels of all streams in a row sharing a common paddle rod. Further descriptions of the streams can be found in Carder and Hoagland (1998), and Spawn et al. (1987). Modifications to the stream design included:

1) a raised platform which consisted of a 28.3 x 58.9 cm wooden board placed over bricks,
2) a lining to cover the platforms and prevent contamination, made of 2.4 x 1.8 m, 6-mil, clear plastic sheet,
3) a brick was placed on each platform to secure leaf packs. The brick was power sprayed with tap water and then soaked in a bucket of Missouri River water to remove any toxins or excess nutrients,
4) a paddle wheel cover constructed of 20-gauge galvanized steel fender and plastic skirting to reduce water loss.

Water was drawn from the Missouri River near Nebraska City, NE, with a Honda centrifugal pump and transported in a 3785-L polyethylene tank. Sediments were allowed to settle within the tank. Approximately 91 L of the water was then pumped in one-third increments to each of the artificial streams, while simultaneously filtered through a 64-μm-mesh net. Distilled water was periodically added to the streams to compensate for evaporation, maintaining streams at their initial water level without altering other water quality parameters. Water current velocity was measured with a Marsh-McBirney, Inc. (Frederick, MD, USA) current meter and maintained at 20

cm/s over the platform where leaf packs were placed in two of the treatments. Sediments collected from two Missouri River field sites were filtered with a 1-mm sieve, mixed, and placed in Petri dishes. Each stream received two Petri dishes of sediment, one from each of the field sites for a total of 124 g of sediment. Water temperature was maintained between 22-24°C. Fluorescent lights which mimicked low light intensities similar to those encountered by leaf packs at field sites (5–48 $\mu mol\ m^{-2}\ s^{-1}$) were operated on a 12 h:12 h light:dark cycle.

Treatments were randomly allocated to streams. Treatments included: 1) a control with no leaves and no invertebrates, 2) leaves without invertebrates, and 3) leaves with invertebrates, with four replicates of the control treatment and six replicates each of the treatments with leaves. Cottonwood leaves were used for the leaf packs, as this is the dominant riparian tree species along the Missouri River. Abscised and dried leaves were collected in the fall to mimic yard waste as a potential source of organic matter addition to the Missouri River. Leaves were weighed to 5 g and attached with monofilament line. The entire leaf pack was then reweighed to the nearest 0.1 mg and tied to a brick on the platform in the stream. Invertebrates were collected from the Missouri River from 26 leaf cages left at two field sites for 15 days. Upon removal from the river, the leaf cages were placed in aerated plastic tubs and transported to the lab. Prior to this collection, invertebrate composition and density of leaf colonizing invertebrates was determined for leaf cages from four field sites. Information obtained from both the previous and final collections was scaled down for the leaf packs in the artificial streams. Invertebrates were selected and measured to ensure similar relative size per taxon. After reducing the current velocity, invertebrates were placed directly on leaf packs of six streams. Current velocity was then gradually increased to 20 cm/s. The leaf pack community consisted of the following: one each of two species of Ephemeroptera (*Caenis* and *Stenonema*), one trichopteran (*Nectopsyche*), one dipteran (Chironomidae), five amphipods (*Hyallela azteca*), and two gastropods (*Physa*). The

trichopteran Hydropsychidae, although common in the river, was not added to the streams since it may function as a predator and may also tear the plastic lining of the streams. Chironomids were in low numbers, initially and later in the experiment, since they tended to reach maturity quickly and emerge in the laboratory.

1.1.2. *Water Quality Parameters*

Water quality parameters monitored included: temperature, pH, dissolved oxygen (DO), total phosphorus (TP), total nitrogen (TN), and dissolved organic carbon (DOC). Water samples and measurements were obtained on days 0, 3, 7, and 14, with the exception of DOC, which was initially sampled on day 1 rather than day 0. Day 0 was 24 h after the addition of water, sediment, and leaf packs, and day 1 was 48 h after additions. After water samples were obtained for DOC on day 1, macroinvertebrates were placed in the streams on the leaf packs. On each sampling date, paddlewheels were turned off, DO and temperature measured (Yellow Springs Instruments, model 57, Yellow Springs, OH, USA), distilled water added to bring stream water to previous levels to compensate for evaporation, paddlewheels turned back on, and streams allowed to equilibrate for 30 minutes. Paddlewheels were stopped again and pH and temperature measured (Fisher Scientific Accumet®, model 1002, Pittsburgh, PA, USA). Water samples were collected in acid washed, foil-capped flasks for TP and TN, and in acid cleaned, pre-combusted, amber bottles for DOC. Paddlewheels were turned back on and current velocity over the platforms returned to 20 cm/s. Samples for TP and TN were frozen until analysis. TN was analyzed by alkaline potassium persulfate digestion using the methods of D'Elia et al. (1976) and ultraviolet absorption methods from APHA (1985). TP was analyzed with the ascorbic acid method from Lind (1985). Samples for DOC were preserved with mercuric chloride, refrigerated, and samples from day 1 and day 14 were analyzed by the University of Nebraska Water Sciences Lab using a modified version of the

wet-oxidation method from APHA (1989) and a total organic carbon (TOC) analyzer (OI Analytical Corporation, model 700, College Station, TX, USA); samples were filtered through a glass fiber filter and digested in the instrument. Only four samples for DOC from day 1 were taken to the lab for analysis, two controls and two leaf treatments.

1.1.3. *Leaf Packs, Particulates, and Macroinvertebrates*

Leaf packs were removed from streams on day 14. Invertebrates and gastropod egg capsules were collected, the leaves gently rinsed to remove sediments and placed in foil boats to air-dry. Dry mass of the leaf packs was obtained, and the leaves were then thoroughly cleaned for biofilm removal by gently rubbing leaf surfaces by hand under a constant stream of water over a sieve. Leaf fragments, lost by this process, were retrieved with forceps and included with the leaf packs. Leaf packs were then reweighed. An estimate of biofilm dry mass was obtained from the difference between these two weights. Dry masses were obtained after oven drying at 60°C for two days. Contents from the streams were filtered at the completion of the experiment. Invertebrates, sand, and organic matter or particulates, were collected. Invertebrates and material associated with them (i.e. appendages, molts, and pupal exuvia) were collected from the filtrate with the aid of a dissecting microscope. Particulates were elutriated from the sand, washed through two nested sieves (300 μm to 1 mm and >1 mm) and dry masses obtained for both size fractions. The surface area of particulates was then measured within each size fraction with Optimus image analysis software (version 4.1, BioScan Inc., Edmonds, WA, USA). Surface areas of a large sample of particulates were first measured to determine how many particulates from each sample should be measured. CPOM included leaf fragment organic matter (LFOM), 16-256 mm^2, and large particulate organic matter (LPOM), 1-16 mm^2. FPOM included medium particulate organic matter (MPOM), 0.0625-1 mm^2, and small particulate organic matter (SPOM), 5.6 μm^2 to

0.0625 mm^2. Leaf packs and particulates were ashed at 550°C to determine organic matter content. Invertebrates were enumerated and preserved in 80% ethanol for further identification and gut content analysis. Gut content analysis was performed as described by Hershey and Peterson (1996). Guts were removed, placed on a slide with mounting medium and teased with a pin. The coverslip was pressed gently to spread the material for analysis. Categories identified included vascular plant detritus (fibers and particulates), amorphous detritus (stained and unstained), inorganic particulates (i.e. sand), diatoms, globular or gelatinous material, and fungi. A semi-quantitative analysis included relative amounts of gut components, and actual numbers and relative sizes of selected contents (i.e. plant fibers and particulates).

1.1.4. *Data Analyses*

Statistical analyses consisted of ANOVA and Tukey's honestly significant difference using SYSTAT (version 5.0, SYSTAT, Inc., Evanston, IL, USA). The comparisons analyzed included: 1) control versus leaves without invertebrates versus leaves with invertebrates for water quality parameters and organic particulates [dry mass, proportion of particulates of different size fractions, and ash-free dry mass (AFDM)], and 2) leaves without invertebrates versus leaves with invertebrates for leaf mass loss, and leaf biofilm dry mass. Statistics were run on size class percentages of POM. Transformations were not necessary since the means and standard deviations of each size class among treatments were similar; therefore the assumptions of normal distribution and constant variance were not violated, except in one case (LFOM). LFOM control groups contained no particulates in this size range, thus only leaf treatments were analyzed.

1.2. Results

1.2.1. *Water Quality Parameters*

Temperature, pH, DO, and TP did not vary significantly among treatments on any sampling date, and TN was not significantly different through day 7 (Table 1). Thus, mean values are summarized for each treatment for these parameters (Table 2). Variation in DO, on days 3 and 7, was due to transitory problems with water circulation.

Streams with leaf treatments were noticeably stained 24 h after leaf addition, whereas control streams remained relatively clear. The parameters that differed significantly among treatments were DOC and TN by day 14 (Table 1, Fig. 2). When no significant difference existed among treatments, the means were obtained from the combined data (Table 2). Initially, TP values were approximately 54% of TN values, but by day 14 TP values were greater than TN values. By day 14, TP was approximately 2.5 times greater than on day O. TN for leaf treatments had decreased to values similar to the initial concentrations by day 14; however a continued increase was observed for the control, which was significantly higher than leaf treatments by day 14 (Tables 1 and 2, Fig. 2a).

Invertebrates were added after sampling for DOC on day 1; therefore the leaf treatments were combined and compared with the control group. DOC was greater in those streams with treatments that included leaf additions. By day 1, there was a greater difference between these streams and the control groups than by day 14; however, since only two samples were analyzed for each of these two treatments, the difference was not significant ($p = 0.062$). There was a slight decrease in DOC over time in steams with leaf additions, whereas there was a slight increase in DOC in the controls. A DOC value from one stream on day 14 was omitted from the statistics due to a tear in the plastic lining; the larger DOC value reflected this problem.

1.2.2. *Leaf Mass Loss and Appearance*

Leaf mass loss was not significantly different among treatments containing leaves (Table 6). In both cases, the mean mass loss of the leaf packs was 34% after two weeks (Table 3; Fig. 3). The appearance of the leaves from both treatments was very similar. By day 14, all leaves were soft, brittle, and had a biofilm on their surface. Leaves appeared intact, and no skeletonization of the leaves by invertebrates was noted.

1.2.3. *Leaf Breakdown Products*

Biofilm

Leaf biofilm was included since it may contain leaf particulates and leaf leachate material (Table 4, Fig. 3). The biofilm accounted for the largest portion of leaf mass loss; 47% for leaves without invertebrates and 32% for leaves with invertebrates (Table 6, Fig. 4). Although the biofilm dry mass was lower for the invertebrate treatment, the difference was not significant (Table 7).

POM Dry Mass and DOC

Final dry mass of the products is illustrated in Fig. 3. Control values were subtracted from leaf treatment values to gain insight as to how leaf breakdown products related to leaf mass loss (Table 6, Fig. 4). DOC and total particulate organic matter (POM) made up only a small fraction of the total organic matter measured (Tables 4 and 6). DOC was significantly higher in the streams that included leaves (Table 2). DOC accounted for a larger percent of the leaf mass loss, 8% on day 1, than the leaf particulates. By two weeks, POM accounted for less than 1% of leaf mass loss in the leaf treatment and less than 4% in the invertebrate treatment. POM included coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM). The dry

mass of total CPOM (>1 mm) was significantly greater in the invertebrate treatment; however, no significant differences were noted for FPOM (300 μm – 1 mm) dry mass. The results for coarse particulate organic carbon (CPOC) and fine particulate organic carbon (FPOC), obtained from AFDM, were essentially the same as the dry mass results (Table 7). By comparing the experimental groups with the control group, it was apparent that much of the particulates originated from the sediments added to the artificial streams rather than the leaf packs (Table 4, Fig. 3).

1.2.4. *POM Surface Area*

A pattern similar to POM dry mass was noted for CPOM and FPOM when the particulates were separated into four size fractions based on their surface area; however, surface area measurements revealed a smaller percent of CPOM for the invertebrate treatment, and a larger percent of CPOM for the control and leaves without invertebrates treatments. Most of the leaf particulates, 70–81%, were MPOM (0.0625-1 mm^2), whereas LPOM (1-16 mm^2) made up 19-28%. No significant differences were noted in CPOM, LPOM, FPOM, MPOM, or SPOM among the three treatments and no significant differences in LFOM between the leaf treatments (Tables 5 and 7, Fig. 5).

1.2.5. *Macroinvertebrates*

Detailed invertebrate survival rates were not obtained since the artificial streams were not enclosed. However, many invertebrates were recovered and the following survival estimates were made: 1) >50% of the *Caenis*, 2) >33% of the *Stenonema*, also found four late or final instar molts, 3) 100% of the *Nectopsyche*, 4) >67% of the Chironomidae (one pupa, two pupal exuviae, and one adult), and 5) 75% of the *Physa*. Approximately 67% of the streams showed an increase

in the *Hyallela azteca* population, and many of the females were gravid. *Physa* egg capsules were found in all but one stream, where *Stenonema* still existed. Most of the invertebrates that were still living in the streams were found on leaf packs or bricks; however, more than half of the *Physa* were found on the plastic lining the streams where a biofilm was evident.

Gut contents consisted primarily of amorphous FPOM and inorganic particulates (i.e. sand) followed by orange, rust, and brown globular material and fungi. FPOM was separated into two categories; that stained by leaf leachates and unstained FPOM. Where the stained FPOM (generally orange, rust, or brown) occurred, globular or gelatinous material and fungi were commonly noted. Pennate diatoms were only noted in one *Nectopsyche* gut. Infrequently, plant fibers and particulates that may have originated from the leaf packs were included in the gut contents: 1) 19% of *Hyallela azteca* contained one to three fibers, 5-6% of these also had leaf particulate(s), 2) 22% of *Physa* had one to three fibers along with leaf particulates, one of which appeared to be a single layer of cells from the outermost leaf surface, 3) the only *Stenonema* in larval form contained one fiber and a leaf particulate, 4) 50% of the *Nectopsyche* contained leaf particulates, 33% (two Individuals) of which appeared to contain a sheet of cells as described for the *Physa*, 33% of these also had a fiber. No evidence of leaf material was noted in *Caenis*. All plant fibers and possible leaf particulates were very small and made up the smallest fraction of the total gut contents. Sand grains were more common than plant fibers and leaf particulates.

1.3. Discussion

1.3.1. *Water Quality*

Leaf addition did not significantly affect temperature, pH, DO, or TP over a two-week period (Table 1). Slight increases and decreases in DO within the streams correspond to slight changes in water temperature. However, these values were within the ranges noted at sites where

organic matter addition has been proposed during the summer months, i.e. 8.2-8.5 mg/l DO and 22-24°C (Table 2, Hesse et al. 1989). Stream pH remained similar to values observed at Missouri River field sites; initial pH of our streams and an unchannelized river reach was 8.6, final pH of our streams was 8.4, and pH of a channelized river reach was 7.9 (Table 2, Schmulbach et al. 1992). The increase in TP and changes in pH were due to abiotic and/or biotic factors associated with the river sediments and water added to the streams. This also appears to hold true for TN up to day 7 (Table 1, Fig. 2a). It is likely that the water in our streams, collected from the Missouri River near Nebraska City, initially contained a larger concentration of TP and TN than those sites proposed for organic matter addition. It has been shown that mean TP and TN concentrations are lower in unchannelized reaches than channelized reaches, and that Lewis and Clark and Francis Case Lakes, which lie on either side of an unchannelized reach, are phosphorus limited. In fact, water entering the unchannelized reach from reservoirs is nearly devoid of TP and TN (Hesse et al. 1989, Schmulbach et al. 1992). Consequently, decomposition rates would be expected to differ between the two reaches and result in a more rapid rate of leaf decomposition in our microcosms than proposed sites of organic matter addition.

By day 14, leaf addition resulted in the removal of a significant amount of TN from the water column to values similar to initial concentrations (Tables 1 and 2, Fig. 2a). DOC was greater in the leaf treatments after 48 h after leaf addition and significantly greater by day 14; however, DOC had increased in the control and decreased in the leaf treatments. Initial mean DOC for the leaf treatments (4.9 mgC/l) was very similar to an unchannelized reach of the Missouri River (4.8 mgC/l). Final mean DOC for these same treatments (4.5 mgC/l) was more similar to a channelized reach (4.6 mgC/l) (Tables 1 and 2, Fig. 2b, Schmulbach et al. 1992).

1.3.2. *Leaf Processing*

Cottonwood leaves and those of other taxa of Salicaceae are considered to have intermediate breakdown rates (k = 0.005; Webster and Benfield 1986). Changes in DOC, TN, and leaf condition at the end of the study, give insight into leaf processing.

Phase 1: Rapid Leaching

The first phase in leaf processing is rapid leaching of most of the soluble substances of the leaves, which generally occurs in one to two days (Kaushik and Hynes 1971). This explains the increase in DOC within 48 hours of leaf addition. Leaching may account for the majority of leaf mass loss. Mean mass loss for both leaf treatments was 34% after two weeks, with rapid breakdown rates (leaf treatment k = 0.030, leaf/invertebrate treatment k = 0.029). Hill et al. (1992) found that cottonwood leaves placed in a prairie stream had a 31% leaching loss after 48 hours.

Phase 2: Microbial Colonization

The second phase involves microbial colonization of the leaves. Stream temperature, pH, phosphorus, and nitrogen have been shown to affect fungal colonization (Kaushik and Hynes 1971). In our streams, these parameters were within ranges that should not have inhibited fungal colonization. Fungi utilize inorganic nitrogen compounds from the water, thereby increasing the protein content of the leaf (Barlocher and Kendrick 1975). Increased microbial biomass in our streams containing leaves, would explain the significant decrease in TN from the water column by day 14. This is consistent with a study on a Kansas prairie stream in which the nitrogen concentration of leaves increased during decomposition (Tate and Gurtz 1986). As leaves become conditioned, their quality as a food source increases for detrital feeders. Microbial cells are easily digested and high in protein, and microbial catalysis decomposes leaf compounds into more

digestible subunits (Barlocher and Kendrick 1975). The decrease in DOC by day 14 in streams with leaves may also indicate an increase in microbial biomass. It has been shown that allochthonous DOC supports bacterial growth (Wetzel and Manny 1972 In Macan 1974, Sobczak 1996). By the end of the study, leaves were soft, brittle, and a biofilm was evident on their surface. It has been long known that leaves become softened by microbial activity (Suberkropp and Klug 1980). Stream biofilms, consisting of polysaccharide, a glycoprotein matrix, fungi, bacteria, algae, and FPOM can affect leaf decomposition and provide a food source for detritivores (Maltby 1992, Sobczak 1996). The presence of macroinvertebrates reduced leaf biofilm dry mass (Table 4, Fig. 3); however, the decline was not significant relative to streams lacking macroinvertebrates (Table 7).

Phase 3: Invertebrate Consumption

Invertebrate consumption has been described as the third phase of leaf processing (Kaushik and Hynes 1971). The invertebrate community was based on those found on leaf packs in the Missouri River. Feeding modes of this community consisted mainly of collector-gatherers and scrapers. *Nectopsyche* can function as shredders but are herbivores rather than detrivores (Wiggins 1996). Some species of chironomids may also function as shredders (Coffman and Ferrington 1996), but they were not well represented in this study. However, in a tall grass prairie stream in Kansas, chironomids were the numerically dominant insect on leaf packs and it was concluded that macroinvertebrates probably had little effect on leaf decomposition rates (Tate and Gurtz 1986). In addition, a study conducted on the Missouri River in northeastern Nebraska found that although several functional feeding groups of chironomids were represented, this family belonged primarily to the collector-gatherer group (Troelstrup 1985). With the exception of filterers, the feeding modes of this community were representative of the major genera of Missouri River macroinvertebrates (Hesse et al. 1988).

Invertebrate Gut Analyses

Gut content analyses revealed that amorphous FPOM and inorganic particulates (i.e. sand) were the main materials consumed, followed by fungi and stained globular or gelatinous material, which was likely biofilm material. In his gut analyses, Troelstrup (1985) noted that POM was the predominate food item for most Missouri River macroinvertebrate taxa. Of the macroinvertebrates included in our study, he found: 1) Heptageniidae (including *Stenonema* and *Stenacron*) contained a mean of 93% POM and 13% inorganic material, 2) *Caenis* contained 76% POM and 3% inorganic material, and 3) *Hyallela azteca* contained 79% POM and 6% inorganic material. FPOM that was not stained by leaf leachates was likely to have been collected from bricks and the plastic lining our streams. In those invertebrate guts where FPOM was stained by leachates, fungi and globular material were also noted. The latter, in combination with the fact that leaves appeared intact and not venated, indicate that invertebrates were feeding on leaf biofilm, not on the leaves. Small fibers and leaf particulates were found infrequently and when present made up only a very small fraction of the total gut contents. Since even sand was more common, it appears that the leaf material was not being selected for. The *Nectopsyche* may be an exception, as approximately 50% appeared to contain leaf material and in somewhat larger quantities, although still a small fraction of the total gut contents. It is possible that at least some of this material originated from the sediments added to the stream as they were all less than 1 mm and so would have passed through the screen when the sediments were sieved prior to placement in the streams.

Detritus as a Food Resource

Detritus has been shown to be an important food resource for many aquatic insects. As Rong (1993) notes, many authors have shown that "allochthonous materials serve as food for many

members of almost all important groups of aquatic organisms, in many cases providing the bulk of their diet". Troelstrup (1985) pointed out that 12 of 14 Missouri River macroinvertebrate taxa belong to the collector-filterer and collector-gatherer groups. He added that along with the observation of the predominance of dead particulate organic matter in the diets of all but one species of his invertebrates, his study supports predictions of the River Continuum Concept, which "predicts high availability of fine particulate organic matter in large lotic systems like the Missouri River". Invertebrates of this type of system should be dominated by collectors, which efficiently utilize FPOM (Cummins 1974). Therefore, although detritus may be an important food resource for Missouri River macroinvertebrates, shredding activities of leaf material by the invertebrates should be rare.

1.3.3. *Macroinvertebrate Success*

In general, macroinvertebrates appeared successful within the streams, based on growth, survivorship, and fecundity. Many of the invertebrates survived the two-week study, and most of *Stenonema* and Chironomidae appear to have reached maturity. *Hyallela azteca* and *Physa* were reproducing as was noted by an increase in amphipod populations, gravid female amphipods, and physid egg capsules. Although an attempt was made to avoid late instars of the aquatic insects, some had reached maturity during the study and emerged from the streams. This was evidenced by the presence of pupal exuviae and late instar molts, which may have impacted leaf decomposition rates. However, as noted *Hyallela azteca* increased in two-thirds of the streams, so new community members were added, and leaf mass loss was slightly higher in those streams. Where both of the *Physa* survived in these same streams, leaf weight loss was even greater. However by day 14, five of the nine surviving snails were found on the plastic lining the streams rather than on

leaf packs. Webster and Benfield (1986) noted that leaves in laboratory streams with snails lost as much as six times the mass of leaves in channels without snails.

1.3.4. *Leaf Breakdown Products*

Leaf Mass Loss

The addition of common Missouri River invertebrates did not significantly contribute to leaf processing over the two-week period. Leaf mass loss and final organic carbon content of the leaves were not significantly different between the leaf treatments (Table 7). In both cases, the mean mass loss of the leaf packs was 34% by two weeks (Table 3, Fig. 3). This is consistent with the belief that in large rivers that receive relatively small amounts of allochthonous inputs, macroinvertebrates play a minimal role in leaf decomposition (Webster and Benfield 1986). These results are consistent with those of Bird and Kaushik (1992) who concluded that leaf mass loss was governed by physical abrasion and microbial activity at an agricultural section of a stream.

Particulate Organic Matter

When compared with the control groups, it was apparent that much of the POM originated from sediments and water added to the streams (Table 4, Fig. 3). POM accounted for only a small fraction of leaf mass loss, less than 1% in streams without invertebrates and less than 4% for streams with invertebrates (Table 6, Fig. 4). Most of the particulates from the streams were in the size range of FPOM, as is noted by dry mass, organic carbon content, and surface area (Table 5, Fig. 3 and 5). POM in this size range should be ideal for collectors (filterers and gatherers) (Vannotte et al. 1980), which represent the majority of the Missouri River macroinvertebrates. Leaf addition did not significantly increase any of our measurements of FPOM present in the streams, for either treatment, by day 14. However, measurements of FPOM should be underestimated due to the larger mesh size of the nested sieves. This would include SPOM and

some of the smallest MPOM. In addition, FPOM was present in relatively large quantities in invertebrate guts and was likely consumed throughout the experiment. Additional factors that would have reduced actual POM measured in streams include: 1) particulates attached to invertebrates and egg capsules that had been removed from the stream, 2) cases of Nectopsyche, which included POM, showed at least modest increases in length, indicating they had used POM to enlarge their cases, and 3) microbial degradation of POM. MPOM accounted for 70-81% of POM based on surface area.

LPOM (within the CPOM size class) accounted for 19-28% of POM on day 14. A significantly greater amount of CPOM was generated by the presence of macroinvertebrates, as shown by dry mass and CPOC (from AFDM) (Table 7, Fig. 3). However, this difference may be due to material that originated from sources not directly related to the leaves. For example, although filtrates from the streams were observed under a dissecting microscope, material originating from invertebrates (i.e. body parts, molts and pupal exuviae) may not have been recognized as such and removed. Invertebrate feces may have also contributed to the total particulates, and may be another important food resource for invertebrates (see Richardson and Neill 1991). Surface area measurements resulted in a greater percent of CPOM than dry mass for controls and leaves without invertebrates, and a smaller percent of CPOM for leaves with invertebrates (Table 5). This resulted in no significant difference in CPOM, as a percent of total POM, between the leaf treatments for surface area (Table 7). In any case, there was no significant difference in leaf mass loss between streams with and without invertebrates. Therefore, we can conclude that the invertebrates did not make a significant contribution to leaf breakdown rates.

Dissolved Organic Carbon

DOC for the entire stream accounted for a greater amount of leaf mass loss than did particulates, approximately 8% for both leaf treatments 48 hours after leaf addition (Table 6, Fig. 4). This estimate is likely conservative since DOM can be converted to FPOM through flocculation or adsorption to other surfaces. Additionally, stream bacteria consume DOM. Estimated leaf biofilm dry mass accounted for the largest percent of leaf mass loss, 47% for leaves without invertebrates and 32% for leaves with invertebrates (Table 6, Fig. 4). The biofilm may have contained a significant amount of leaf leachate and POM. Lester et al. (1995) found organic layer carbon on stone surfaces in willow shaded sites to contain up to 66% of carbon from willows and up to 78% fine particulate organic layer carbon from willows. Biofilm development on substrata has been shown to enhance colonization by benthic macroinvertebrates thus leading to greater densities (Hax and Golladay 1993). Bacterial specialists such as filter feeders and biofilm grazers (Meyer 1994) should especially benefit from an increase in DOM and biofilm development.

1.3.5. *Field Studies on Leaf Litter Processing*

Most studies have been conducted on low order and forested headwater streams (e.g. Johnson et al. 1995). There is evidence that suggests that macroinvertebrates are not as important in leaf decomposition for large rivers and prairie streams, such as the Missouri River which is an 8^{th} to 9^{th} order stream. However, allochthonous material may still offer important food resources to various functional feeding groups despite a lack of shredding macroinvertebrates. The following studies support our findings and may offer further insight into Missouri River food web dynamics.

Invertebrate versus Microbial Contribution to Leaf Degradation

A study conducted on a 4^{th} and 5^{th} order prairie stream in Kansas during the summer concluded that macroinvertebrates contributed little to leaf degradation and that microbes were the

most important biotic contributors (Smith 1986). Indirect feeding of collector-scrapers, leaching and other physical losses were also likely to be important in leaf mass loss. It was suggested that macroinvertebrate usage of the leaf material was habitat based, i.e. used for protection and for its ability to collect FPOM and periphyton (Smith 1986). Bird and Kaushich (1992) also concluded that physical abrasion and microbial activity governed leaf weight loss in an agricultural section of a stream. Similar results were obtained for 3rd order intermittent and perennial Kansas prairie streams. Initial leachates from the leaves were suggested as a possible nutrient input; however, as the leaves decompose they may act as a nutrient sink and compete with other ecosystem processes (Tate and Gurtz 1986). Macroinvertebrates colonizing leaf packs consisted of few if any shredders, which probably had little impact on leaf decomposition rates. Chironomids were the most abundant insects. However, when the study was repeated two years later, decay rates had doubled due to the presence of *Tipula,* which were not found on leaf packs in the previous study (Tate and Gurtz 1986). Hill et al. (1992) state that although shredder density is low in streams of the southern Great Plains, organic matter is processed rapidly. Again, microbial activity is suggested as the most important biotic agent of leaf decomposition in these streams and microorganisms were noted to cause 10-66% of the leaf mass loss. Macroinvertebrate densities were low and consisted of 60% scrapers (mainly *Physa*), 36% collector-gatherers (chironomids and *Hyallela*), and 3% shredders (*Tipula* and crayfish).

Litter Retention

CPOM cannot be efficiently used by macroinvertebrates if the material is not retained. As Webster et al. (1994) stated, the retention of CPOM decreases as the stream size increases due to a decrease in debris dams, specifically woody debris, and greater water depth. It is possible that it is the lack of detritus retention that is responsible for the lack of detritivore fauna (Webster and

Benfield 1986). In the Missouri River, desnagging of the channels has further decreased debris dams and water depth has increased due to channelization and an altered hydrologic regime. Faber (1999) notes that the loss of floodplain trees combined with the loss of areas where snags can accumulate (i.e. side channels, along inside bends or behind sandbars and islands) has contributed to an 80% decline in food resources for Missouri River inhabitants. Dobson et al. (1995) increased litter retention and leaf litter inputs to two low order streams in mid-Wales, which resulted in large increases in detrivores. It was believed that plastic traps would have eventually resulted similarly, as naturally occuring detritus was more abundant than leaf material. It was concluded that the increased retention was likely as important as the increase in leaf litter inputs.

Detrital Manipulations

Detrital manipulations have been conducted on low order streams. Richardson and Neill (1991) added leaf material to experimental channels adjacent to a 2nd order stream, which led to an increase in collector densities as a whole; however, no treatment effect was noted on densities of any single taxa or species richness. The response was detectable within two months and was attributed to greater survival rates. It was suggested that the response was due to an increase in FPOM due to feeding activities of shredders and included shredder feces as a potential food resource which may be higher energetically and nutritionally compared to background FPOM. Although non-significant, Chironomini, Simuliidae, miscellaneous Trichoptera, and Copepoda increased to the largest extent. Allochthonous material can serve as an important food resource even without specialized shredders. Lester et al (1995) illustrated this in second order streams of New Zealand. They suggested that microbes and physical processes convert CPOM to a form where other functional feeding groups can utilize it. Late instar insects at shaded sites were found to contain 8-74% body carbon from allochthonous material and those at open sites contained

0-23%. More than half of the body carbon from some genera was from willows. What effect allochthonous inputs would have on large rivers like the Missouri is essentially unknown.

1.3.6. *Summary*

Leaf decomposition resulted primarily from chemical leaching and microbial activity, not macroinvertebrate feeding activities; DOC increased significantly as a result of leaching and TN decreased significantly after two weeks. Leaf addition appears to provide a food resource indirectly through biofilm development, and possibly through flocculation of DOM to FPOM, sufficient to support the survivorship, growth and reproduction of invertebrates. In general, it appears that leaf addition did not negatively impact water quality; however, the suggested increase in microbial biomass may be of concern. If microbes become too abundant, the period over which POM is available to detrivores could be greatly reduced (Maltby 1992). In addition, it has been shown that filamentous bacteria such as *Sphaerotilus* and *Leptothrix* bloom with modest increases in dissolved nutrients, and then form large colonies which influences the survival of aquatic insects (Lemly 1998). Another concern is the possible increase in water-borne pathogens (Leff and Lemke 1998). Doubling times for suspended bacteria in large rivers is rapid (hours to days) and growth can exceed export (Allan 1995).

Initial leachates from the leaves may be the most significant nutrient contribution that the leaves make. Through flocculation, DOM can be converted to FPOM and consumed by invertebrates. Microbes may utilize DOM, which then becomes available to invertebrates. DOM may also adsorb to sediments that are then ingested by invertebrates. With respect to the initial question "Will the addition of large amounts of terrestrial plant material to the Missouri River increase secondary production?" this research suggests that there is potential. However, it is well known that the Missouri River suffers from multiple alterations. The addition of terrestrial

material alone may not produce the desired effects. Organic matter addition combined with other river management tools, i.e. regarding retention and habitat, may offer significant improvements to the river that may enhance secondary production to levels beneficial to fish and other predators that depend on them as a food resource. However, there are other concerns to be considered, such as the potential for increases in microbial biomass, breakdown products of organic matter and their reactivity with increased UV, accumulation of refractory material, and increases in invertebrate pest species.

It is possible that if the study had been conducted for a longer period of time, the effects of macroinvertebrates would have been more significant. Preliminary lab experiments, in which amphipods and few gastropods were placed in aquaria with cottonwood leaves, support this contention (Rager, unpub. data). In this preliminary experiment, outer leaves of the leaf packs had been venated by the invertebrates over a longer period of time, and biofilm development on the leaves were not as pronounced as in the final experiment. By day 14, leaves in the final experiment had become soft and brittle and thus more susceptible to mechanical breakdown by invertebrate activity. It is also important to recall that most insects are opportunist feeders, and that feeding activities of detrivores such as amphipods and snails that scrape or rasp tissues may contribute to leaf decomposition through venation of leaves (Anderson and Sedell 1979). It is possible that our leaves were not yet fully conditioned by day 14 and that this affected invertebrate feeding. A study conducted in 2nd to 4th order prairie streams in Texas included observations of the decomposition of cottonwood leaves. It was noted that microbial respiration increased and peaked by the 28th day of incubation and then declined thereafter; however, macroinvertebrate densities were low and microbes were the most important biotic decomposer of the leaves (Hill 1992).

It is unlikely that leaves or leaf packs in the Missouri River would be accessible to macroinvertebrates for even two weeks. There is a lack of debris dams in the Missouri River, and

CPOM transported directly downstream is inefficiently used. When leaves stop floating down the Missouri due to an obstruction or sink, they are likely to be rapidly buried in the sediments. In the sediments, leaves tend to become black and leathery due to anoxic conditions and may be of little nutrient value to invertebrates or unavailable. Gawne (unpub. data) has conducted research in the Missouri River, which addressed cottonwood leaf and grass decomposition and laboratory research on the impacts of burial by sediments, which support these contentions.

1.3.7. *Future Research*

The dynamics of large rivers in general and prairie streams in particular, continue to be poorly understood. Further compounding the challenge of understanding Missouri River dynamics is the extent of management that has been conducted on the river by federal agencies. Six headwater dams have left nearly one-third of the river impounded, another third is channelized, and the hydrologic cycle has been altered in the remaining (Hesse et al. 1989). In addition, "by 1980, more than 90% of the river's floodplain forests, prairies and wetlands had been converted for agricultural uses", and currently less than 10% of the floodplain is inundated during flooding events (Faber 1999).

Further research should be conducted over longer periods of time, conceivably over two months of each season, in the Missouri River and in depositional zones and backwater areas, which have been lost due to river regulation. In addition to understanding allochthonous DOM dynamics in the Missouri River, research should focus on further decomposition studies and invertebrate colonization and utilization of plant material. It is possible that immigration of shredders may occur if there is sufficient substrate available. Leaf material may also provide temporary habitat and alternate food resources to invertebrates. The contribution of wood should also be studied. Wood is a more stable substrate than leaves and may act as an important retention device for

organic material. Wood may also supply food resources to the invertebrate community. A study conducted in a Georgia river found that submerged wood made up 4% of the total habitat and supported 60% of the invertebrate biomass (Hesse and Schmulbach 1991). The type of organic matter that serves as the primary energy source in lotic systems and where this material originates is largely unknown. This is important since stream productivity and species composition of the biotic community are affected by the source of energy (Vannote et al.1980). Stable isotope analysis can help to determine energy sources and flows through lotic food webs. Established methods of this analysis can be found in Sullivan and Moncreiff (1990) and Lester et al. (1995). In addition, research on food preferences, and effects of certain food resources on invertebrates (i.e. growth, reproduction and mortality) are likely to be important. The determination of the origin of important energy sources, i.e. grass, trees, macrophytes, and phytoplankton, and its utilization by consumers could aid in the development of powerful river management tools for increasing secondary production in rivers.

Questions that merit further research include: 1) How would an increase in terrestrial DOM impact microbial biomass? 2) If microbial biomass were altered, how would this affect other organisms in the river? 3) Would simuliids, known consumers of DOC and known disease vectors, increase to problematic numbers? 4) What is the potential of organic matter breakdown products in combination with increased ultraviolet light for creating hydrogen peroxide in the river? And 5) Would organic matter addition significantly increase polycyclic aromatic hydrocarbons (PAHs), which are a natural component of decaying organic matter (e.g. leaves). Although the effects of PAHs on lotic ecosystems have not been extensively investigated, they are known to be toxic to many organisms, causing cancer and genetic defects. Benthic organisms ingest PAHs with sediments and bioaccumulation up the food chain is possible. The amount of allochthonous

material that could be added to the river without detrimental effects should also be investigated. Bacterial infestation of aquatic insects should be used as a bioindicator of nutrient enrichment, especially since it can affect insect mortality (Lemly 1998). Ephemeroptera and Trichoptera are among the preferred specimens for detecting filamentous bacterial growth (Lemly 1998) and are relatively common in the Missouri River. There may also be concern for the few existing backwaters and wetlands. It has been noted that accumulations of unprocessed organic matter contribute to the drying up of floodplain margins and the disappearance of fluvial backwaters (Pattee and Chergui 1994).

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Table 1. Summary statistics (p-values) of water quality parameters during the two week study; n = 16 and df = 2, with the following exceptions; n = 15 for TN (day 3) and DOC (day 14), and n = 4 df = 1 for DOC (day 1). Invertebrates were added after sampling for DOC on day 1, therefore the leaf treatments were combined and compared with the control group. NS indicates parameters not sampled, NA indicates samples not analyzed, and * indicates that leaf addition had a significant impact on the parameter. The data was analyzed with Tukey's HSD when a significant difference was indicated by ANOVA. No significant differences existed between the leaf treatments.

	ANOVA					Tukeys HSD		
Parameters	**Day 0**	**Day 1**	**Day 3**	**Day 7**	**Day 14**	**Day 14 control vs leaf**	**Day 14 control vs invertebrate**	**Day 14 leaf vs invertebrate**
Temperature	NV	NS	0.78	0.50	0.88			
pH	0.24	NS	NS	0.24	0.20			
DO	NV	NS	0.48	0.90	NV			
TP	0.20	NS	0.39	0.72	0.46			
TN	0.27	NS	0.70	0.36	0.00*	0.04*	0.01*	0.75
DOC	NS	0.06	NA	NA	0.00*	0.00*	0.00*	0.31

Table 2. Summary of water quality parameters during the two-week study. Means (± SD) were obtained from the combined data when leaf and/or invertebrate addition had no significant impacts. The median is given for pH. NS indicates parameters not sampled, NA indicates samples not analyzed, and * indicates that leaf addition had a significant impact on the parameter.

Parameters	**Day 0**	**Day 1**	**Day 3**	**Day 7**	**Day 14**
Temp. (°C)	23 (0.0)	NS	22.3 (0.2)	22.8 (0.3)	24.3 (0.2)
pH	8.6	NS	NA	8.4	8.4
DO (mg/l)	8.4 (0.0)	NS	8.5 (0.2)	8.5 (0.1)	8.2 (0.0)
TP (µg/l)	337.7 (52.2)	NS	504.6 (70.5)	587.3 (85.3)	833.0 (90.4)
TN (µg/l)	619.7 (91.6)	NS	650.7 (127.4)	723.0 (88.1)	*
Leaf trts					601.5 (61.9)
Control					729.4 (62.2)
DOC (mgC/l)	NS	*	NA	NA	*
Leaf trts		4.90 (0.49)			4.52 (0.17)
Control		3.39 (0.28)			3.70 (0.24)

Table 3. Leaf mass loss in grams (± SD). Initial dry mass was approximately 5 grams. Final leaf organic carbon (LOC), obtained from ash-free dry mass of the leaf packs, is also included.

Treatment	Final dry mass	Mass loss	Mass loss %	LOC
Leaves	3.29 (0.21)	1.71 (0.21)	34.2 (4.2)	2.91 (0.18)
Leaves with invertebrates	3.31 (0.21)	1.69 (0.21)	33.7 (4.2)	2.95 (0.18)
Leaf treatments combined	3.30 (0.20)	1.70 (0.20)	34.0 (4.0)	2.93 (0.17)

Table 4. Leaf breakdown products in grams per stream (± SD)

	Control	Leaves	Leaves with invertebrates	Control and Leaf combined	Leaf treatments combined
CPOM dry mass	0.008 (0.008)	0.010 (0.005)	0.032 (0.011)	0.010 (0.006)	N/A
CPOC (AFDM)	0.004 (0.003)	0.006 (0.003)	0.018 (0.007)	0.005 (0.003)	N/A
FPOM dry mass	0.045 (0.012)	0.052 (0.017)	0.084 (0.041)	0.049 (0.015)	N/A
FPOC (AFDM)	0.016 (0.009)	0.015 (0.007)	0.029 (0.015)	0.016 (0.007)	N/A
Leaf biofilm dry mass	N/A	0.801 (0.377)	0.543 (0.217)	N/A	0.678 (0.323)
DOC day 1	0.307 (0.025)	0.443 (0.044)	0.443 (0.044)	N/A	N/A

Table 5. Leaf particulates: Percentage of total particulate organic matter (± SD)

Leaf Particulates	Control	Leaves	Leaves with invertebrates
No. particulates msrd for surface area (SA)	413	515	584
% CPOM (dry mass)	13.8 (10.4)	16.3 (6.4)	30.2 (11.4)
% CPOM (S.A.)	18.6 (9.7)	20.6 (8.6)	28.6 (5.1)
% LFOM (SA)	0.0 (0.0)	0.4 (0.6)	0.9 (0.4)
% LPOM (SA)	18.6 (9.7)	20.2 (8.6)	27.7 (5.2)
% FPOM (dry mass)	86.2 (10.4)	83.7 (6.4)	69.8 (11.4)
%FPOM (SA)	81.4 (9.7)	79.4 (8.6)	71.4 (5.1)
%MPOM (SA)	80.8 (10.3)	78.5 (8.2)	70.2 (5.4)
%SPOM (SA)	0.7 (0.7)	1.0 (0.9)	1.2 (0.9)

Table 6. Leaf breakdown products in grams per stream and how they relate to leaf mass loss. Control values were subtracted from leaf treatment values.

Treatment	POM	CPOM	FPOM	Leaf biofilm	DOC day1
Leaves					
From leaf packs	0.009	0.002	0.007	0.801	0.136
% of leaf mass loss	0.5	0.1	0.4	46.8	7.9
% of initial leaf mass	0.2	0.0	0.1	16.0	2.7
Leaves with invertebrates					
From leaf packs	0.062	0.024	0.039	0.543	0.136
% of leaf mass loss	3.7	1.4	2.3	32.2	8.1
% of initial leaf mass	1.2	0.5	0.8	10.9	2.7

Table 7. Summary statistics (p–values). Tukey's HSD was applied where ANOVA p-values ≤ 0.10 and df = 2. * indicates that invertebrate addition had a significant impact on final particulate measurements.

Parameter	n	df	ANOVA	Tukeys HSD		
				Control vs Invertebrate	Leaf vs. Invertebrate	Control vs. Leaf
LOC	12	1	0.73			
Leaf mass loss	12	1	0.84			
POM dry mass	16	2	0.01*	0.02*	0.03*	0.90
POC	16	2	0.01*	0.02*	0.01*	0.99
CPOM dry mass	16	2	0.00*	0.00*	0.00*	0.93
CPOC (AFDM)	16	2	0.00*	0.01*	0.00*	0.80
% CPOM S.A.	16	2	0.12			
% LFOM S.A.	12	1	0.15			
% LPOM S.A.	16	2	0.08	0.07	0.34	0.51
FPOM dry mass	16	2	0.09	0.12	0.15	0.93
FPOC (AFDM)	16	2	0.10	0.22	0.11	0.98
% FPOM S.A.	16	2	0.12			
% MPOM S.A.	16	2	0.50			
% SPOM S.A.	16	2	0.52			
Leaf biofilm dry mass	12	1	0.18			

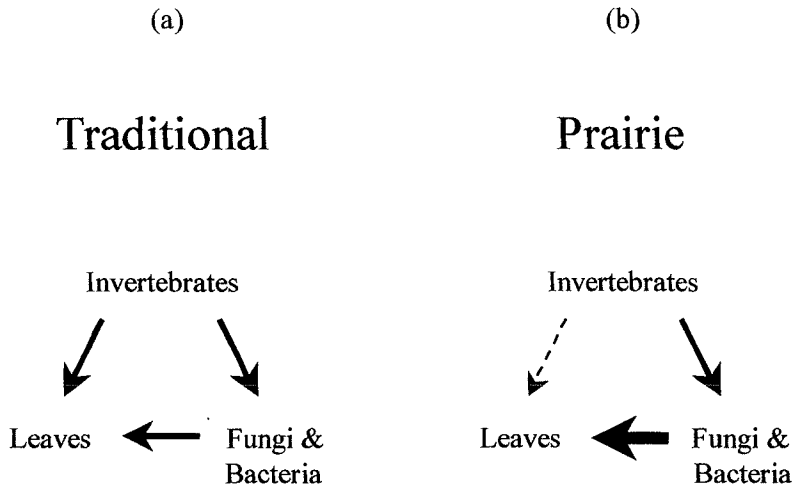

FIG. 1. CPOM – microbial – invertebrate relationship. Thickness of arrow depicts strength of relationship.

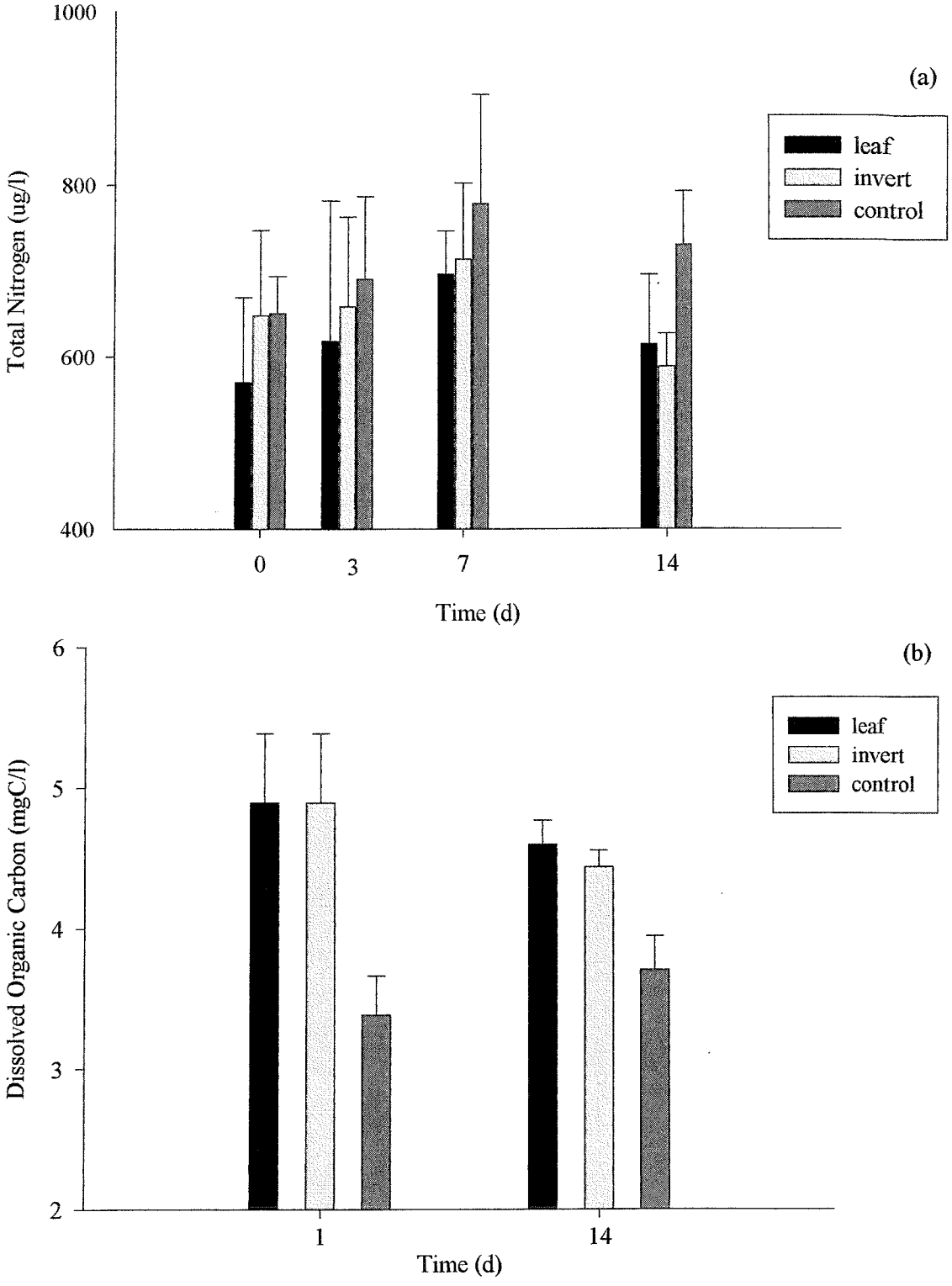

FIG. 2. Total nitrogen (a) and dissolved organic carbon (b) measured over 14 days (+ SD).

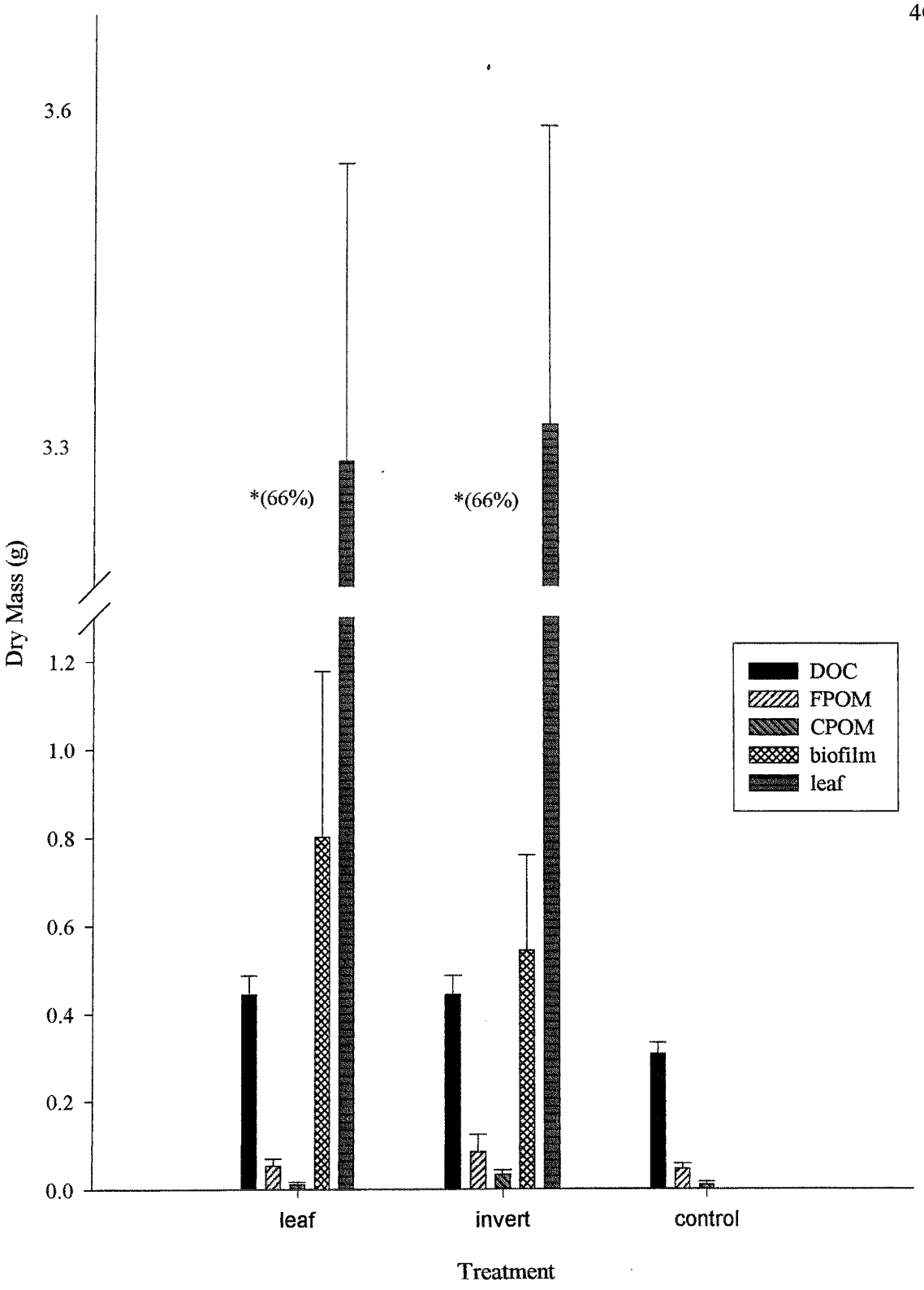

FIG. 3. Mean final mass (+ SD) for leaf packs and leaf breakdown products per treatment. *Leaf packs accounted for 66% of the initial leaf mass on day 14.

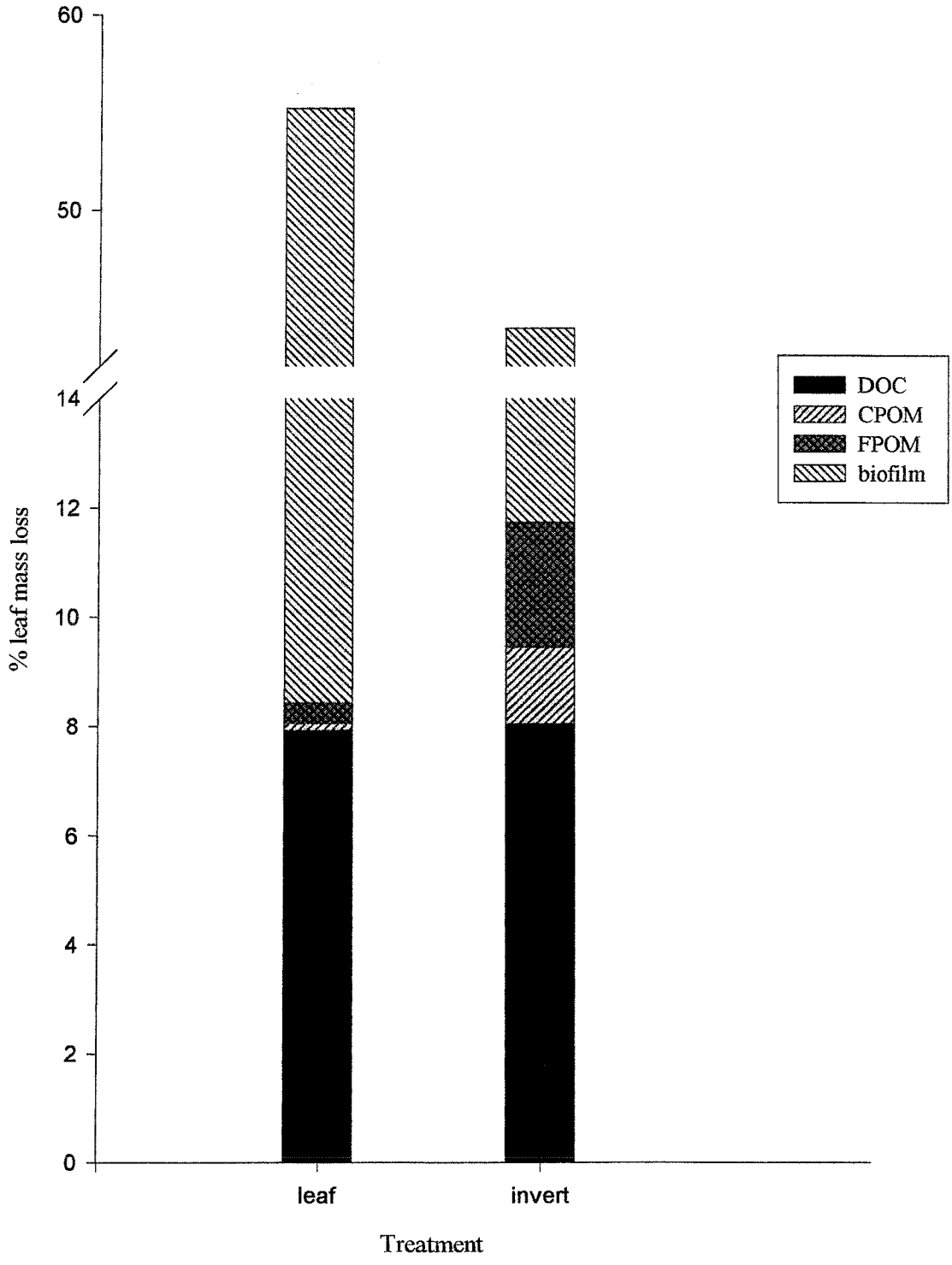

FIG. 4. Percentage leaf mass loss accounted for by leaf breakdown products. Control values were subtracted from leaf treatment values.

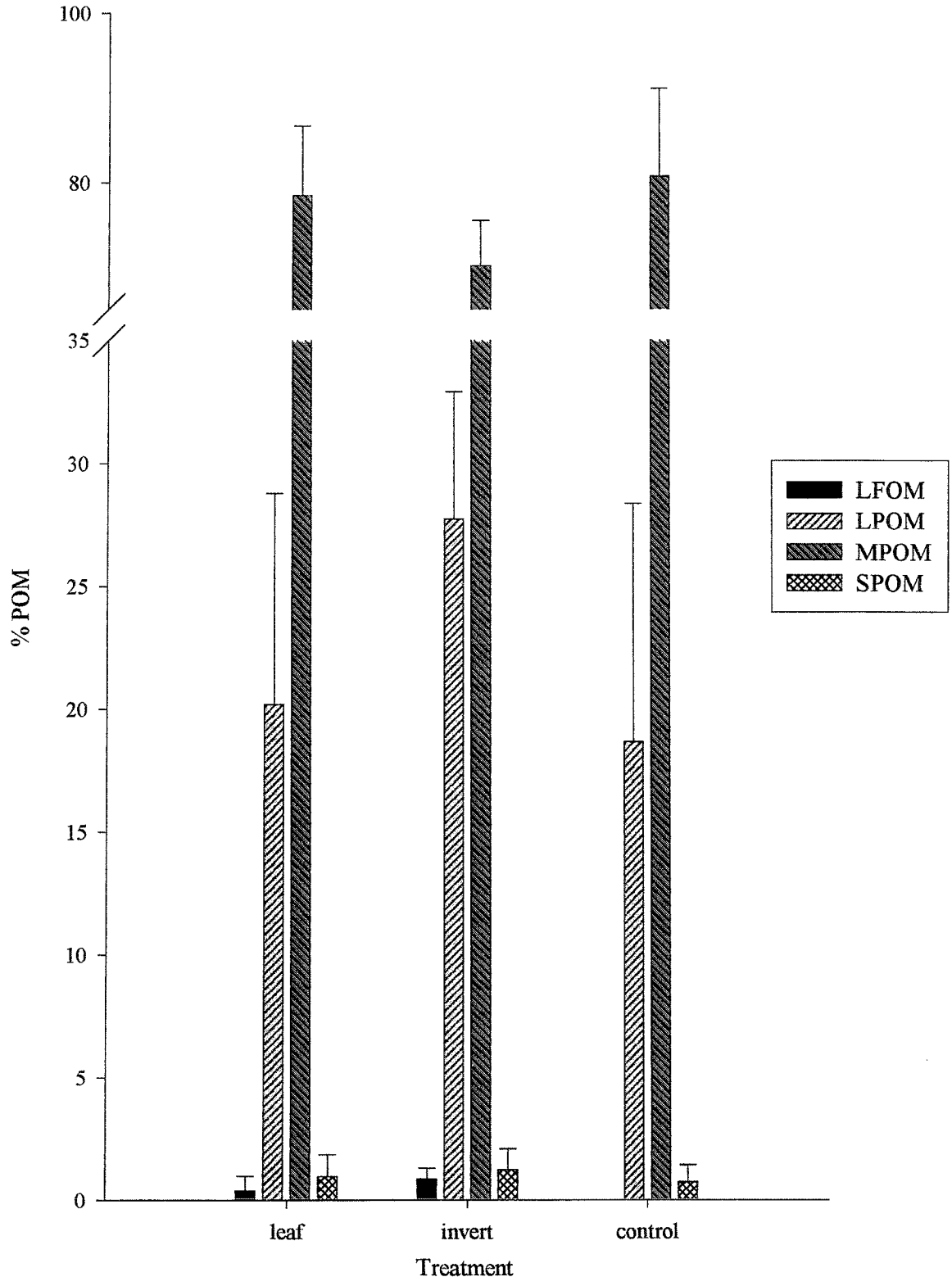

FIG. 5. Leaf particulates: Percentage of total particulate organic matter (POM) (+ SD), obtained from surface area measurements.

CHAPTER 2

Macroinvertebrate utilization of cottonwood leaves and wood in the Missouri River

This field experiment addressed the question: is Missouri River macroinvertebrate use of leaf material nutritionally or habitat-structure based? A wood treatment was added to the experiment because a variety of macroinvertebrates had been observed on wood in the Missouri River. In addition, many previous studies have recognized wood as an important habitat and food resource for many macroinvertebrates.

2.1. Materials and Methods

2.1.1. *Study Sites*

Two sites within an unchannelized reach of the Missouri River in northeastern Nebraska near the town of Niobrara were included in this study (Fig. 1). At these sites, Fort Randall Dam controls the river. The upstream site was approximately 50 km downstream of Fort Randall near the Sunshine Bottom (SB) boat ramp and above the confluence of tributaries. The river channel at SB was simple, approximately 100 m wide and a maximum of 2 m deep. It represented sites with colder water temperatures, slower current velocities, and less associated plant material. The downstream site was near the Niobrara (N) boat ramp and is downstream of the confluence of Ponca Creek. The channel at site N was complex, with an associated wetland, side channels and islands, which supported *Typha* and other macrophytes. The Nebraska Game and Parks Commission have proposed these as possible sites for organic matter addition to increase secondary productivity in the river.

Water temperature at site SB in May, day 2 and 7, was 8°C. An increase was noted by day 30, in June (11.5°C), and again by day 60, in July (19°C). Substrates at site N experienced warmer temperatures than at site SB throughout the study. On d2 and d7, water temperature at

this site was 15°C and increased to 28°C by d30.

Current velocity varied at the individual site level and fluctuations during measurements were common. Thus, a mean (m) of three velocity readings was recorded for each substrate being sampled. Substrates at site SB experienced water velocities of 14 to 25 cm/s ($m = 19 \pm 4$) on d2, and 2 to 25 cm/s on d30 ($m = 14 \pm 9$). Site N had greater velocities: substrates experienced velocities of 36 to 60 cm/s ($m = 46 \pm 9$) by d2, and those measured on d30 ranged from 28 to 47 cm/s ($m = 38 \pm 7$); however, several substrates were buried at this time and were not included in this range.

2.1.2. *Experimental Design*

Macroinvertebrate colonization was observed on four substrates over two months, starting on May 7, 1995. Substrates included: (1) cottonwood (cw) leaves, (2) artificial leaves, (3) cw branches, and (4) artificial branches. Decomposition rates of cw leaves and cw branches were also determined during this period.

Cw leaf packs (L)--Samples consisted of 4.0 g of dried leaves held together with monofilament line. Leaf spacers were created with monofilament line and placed between leaves to increase surface area availability. The samples were then reweighed to the nearest 0.1 mg before placement in the river.

Artificial (nylon) leaf packs (AL)--The size and number of artificial leaves placed in a leaf pack were determined by obtaining the average number and surface area of leaves from several 4-g cw leaf packs. Surface area was determined with a leaf area planimeter. This resulted in 17 artificial leaves per pack with a leaf surface area equal to approximately 22 cm^2 per side. Total surface area, including both sides of the leaves, was approximately 752 cm^2. A pattern was made from a cw leaf with the required surface area, and leaves were cut from textured gray nylon cloth. The leaves were strung together with monofilament line and weighed. Leaf spacers were created as for the cw leaf packs. Mean mass of these packs was 4.9 g.

Artificial wood (AW)--Artificial branches consisted of gray plastic piping scored with coarse sandpaper so that the surface would be more similar to that of cw branches. The size and number of artificial branches was determined by using a surface area equal to half that of leaf packs (one side of leaves). The total surface area of the artificial wood was approximately 181 cm^2. Plastic PVC pipe was cut to 15.24-cm lengths. For each sample, three narrow pipes (O.D. = 0.95 cm) and 4 wider pipes (O.D. = 1.59 cm) were tied together with monofilament line in a manner that allowed for maximum surface area availability; sand was placed in the pipes, and the ends sealed with silicone. The initial mean dry mass of these substrates was 147.6 g.

Cottonwood (W)--Dry cw branches of relatively the same sizes as the piping were fastened together in the same manner as the artificial wood and weighed before placement in the river. The initial mean dry mass of these substrates was 65.9 g.

Experimental units --Twelve replicates of each treatment were tethered in the Missouri at both study sites. Each experimental unit consisted of two metal conduit poles with a 1.5 m chain stretched between them. Four samples, one of each substrate type, were randomly selected and tethered to the chain with monofilament nylon line approximately 30 cm apart. A total of 96 samples were required and extra substrates were placed at these sites in case of loss. The set-ups were then taken into the river channel and the conduit poles hammered into the bottom sediment.

Sample collection --Samples were collected 2, 7, 30, and 60 days after placement in the river, from May 9, 1995 to July 6, 1995, with three replicates of each treatment at each site on each date. On each of the sampling days, three randomly pre-selected replicates of each treatment were removed from the river, cleaned, and organic matter accumulations and invertebrates removed, placed in plastic bottles, and preserved with 10% formalin at the site. It was also noted whether the substrates were buried, submerged, or floating. The cleaned substrates were placed in Ziploc® bags. Current velocity at the site was measured with a Marsh-McBirney (Frederick, MD, USA) current meter. Water temperature was also measured at each

site.

Exceptions to the number of replicates collected occurred on d60 at sites SB and N. At SB, a large portion of the channel moved or was lost due to channel degradation and several experimental units were lost. At this site, two replicates each were obtained for W, AW, and AL, while only one L replicate was found. These substrates were deep under the water surface, as water levels at this site had increased by approximately 1.2 m to a depth of approximately 1.8 m, and they clearly experienced greater velocities than those from previous sampling dates. Conversely, sedimentation was occurring downstream at site N; all substrates were deep in the river bottom and irretrievable.

In addition, one sample had apparently not been preserved for AWN on d7, as indicated by decomposing material and the presence of many live oligochaetes and oligochaete eggs. The unpreserved sample was analyzed, but not included in statistical analyses. Values were corrected by using the mean of the other two replicates for a third replicate.

At site N on d30, substrates were fully or partially buried, but all were accessible. Sand that immediately surrounded these substrates was collected with the samples and weighed.

2.1.3. *Laboratory Protocol*

Sample sorting--All substrates were gently but thoroughly rinsed over a mesh sieve (>300 μm) and any additional material added to the samples. Sand was elutriated from the samples and washed through nested sieves for separation into two size fractions: coarse particulate organic matter (CPOM; >1 mm), and fine particulate organic matter (FPOM; 300 μm –1 mm). Invertebrates were removed with the aid of a dissecting microscope and preserved in 80% ethanol with glycerin.

Dry mass--Final dry mass was measured to determine mass loss, and for the CPOM and FPOM that accumulated on the substrates. Dry mass was also obtained for sand that was

collected with samples on d30 at site N, as an indication of the extent of burial. Dry mass was obtained by drying the material at 65°C for two days before weighing to the nearest 0.1 mg.

Ash-free dry mass (AFDM)—Cw leaves, wood, CPOM, and FPOM, were ashed at 550°C for 4 h to determine organic matter content.

Invertebrates—Identification and trophic relationship (i.e. functional feeding group) were determined with the aid of Merritt & Cummins (1996), Simpson & Bode (1980), Simpson et al. (1983), Darby (1962), Stewart and Loch (1973), Schuster & Etnier (1978), Huggins et al. (1985), Anderson and Sedell (1979) and Cummins et al. (1989). Species composition and abundance of colonizing invertebrates was ascertained and gut analyses performed. Several chironomids collected from the field were also reared to aid in species identification. When a compound microscope was necessary for species identification, the specimens were mounted with CMC-10 mounting medium (USA, WoodDale, IL). Gut contents were also mounted in CMC-10, and categorized as: 1) FPOM; unstained (pale in color) or stained, 2) inorganic particulates, 3) globular/gelatinous material; appeared to be biofilm from the substrates and included fungi, 3) cw leaf and wood particulates, 4) fibers; thin, minute fibers (e.g. root hairs), 5) other vegetation; larger plant material (macrophytes and grass), 6) diatoms, 7) desmids, 8) animal material (chironomids, zooplankton). Upon closer inspection, some of the "fibers" were filamentous algae. Detailed notes on FPOM and biofilm color/staining and appearance of other materials were taken. In addition, the general quantity or proportion of material in the guts was noted. Values of percent larvae with specific gut contents were compared. Comparisons were also made among abundances of invertebrates within various functional feeding groups (FFG) with values representing the maximum percent of individuals within each FFG.

2.1.4. *Calculations and Statistical Analysis*

K-values were calculated to describe leaf and wood breakdown patterns. (k) calculations

used an exponential decay model which assumes that the rate of leaf and wood loss is a constant fraction of the amount of material remaining, and is the negative slope of the line produced by a linear regression of the natural log of percent material remaining against time (Benfield,1996): $k = -\ln(\%M_i/100)/t = day^{-1}$, $\% M_i = M(t_2)/M(t_1) \times 100$ (Tate & Gurtz, 1986). Breakdown rates were categorized as fast ($k > 0.010$), medium ($k = 0.005$-0.010), or slow ($k < 0.005$) (Webster & Benfield, 1986).

Biotic index values were calculated to offer insight into water quality at sites SB and N, and the quality of substrates for invertebrate colonization. The family biotic index (FBI) equation was used to calculate the values (Resh et al. 1996, Hilsenhoff, 1988): $FBI = 1/N \Sigma n_i t_i$; where n_i= number of individuals in a family; t_i = the tolerance score for that family; and N = total number of individuals in the sample; however, we substituted "family" in the equation, for the lowest possible taxon. Tolerance scores were used from a list of tolerance values of Nebraska insects, which also included other aquatic invertebrates (Pruess, unpubl.). Some values for invertebrate families were obtained from Resh et al. (1996). For samples containing > 25 individuals of any species, a maximum of 25 individuals was used for calculations to avoid bias.

Decomposition rates were compared between L and W within and between sites. Statistical anlaysis consisted of one-way ANOVA for comparisons of L and W weight loss on days 2, 7, and 30 between sites. Species composition, abundance, and gut content analysis of colonizing macroinvertebrates were compared among: L vs. AL, W vs. AW, L vs. W, and AL vs. AW, using a one-way ANOVA.

2.2. Results

In the following sections, treatments are abbreviated for simplification: 1) sampling dates, e.g. day 2 as d2, 2) substrates from particular sites, e.g. cottonwood leaf at site SB as LSB, and 3) the most specific treatment as a combination of (1) and (2), e.g. LSB2.

2.2.1. *Leaf and Wood Breakdown Rates*

A. Mass loss

Comparisons of initial versus final mass of L and W indicated significant mass loss of L ($p < 0.0001$) by d30. On d60, two W replicates were collected at site N, but mass loss remained insignificant ($p = 0.041$). This is likely due to variation in initial weights of W, which ranged from 56-78 g. When percent mass loss was analyzed, both L and W experienced significant mass loss by d30.

B. Percent mass loss

Site SB—A significant mass loss of approximately 12% occurred for both L and W by d2 ($p < 0.001$) (Tables 1 & 2). Significant mass loss was also noted from d30-60 for W ($p = 0.004$). By d60, W lost approximately 21% of the initial mass. Only one L replicate was available by d60, which experienced a mass loss of 43%. W required an additional month to lose the same percent of mass as L; WSB60 was similar to LSB30 ($p = 0.072$).

Site N—By d2, a significant mass loss occurred for L (15%, $p = 0.001$) and W (13%, $p < 0.001$). Significant mass loss was noted again from d7-30 for L ($p = 0.01$) and W ($p = 0.004$). By d30, mass loss was approximately 42% for L and 17% for W.

C. Decomposition rates

Decomposition rates are depicted in Fig. 2 as percent of initial mass remaining over time. Using the processing coefficients, decomposition rates were described as fast, medium or slow (Table 2; Webster and Benfield, 1986).

Site SB—Processing coefficients (k) for L and W over 60 d were $k = 0.009$ d^{-1} (medium) and 0.004 d^{-1} (slow), respectively. Both treatments displayed similar rapid initial mass loss from d0-2 ($k = 0.061$ d^{-1} and 0.062 d^{-1}). An especially slow rate of decay followed for

both treatments; W decomposition was slower from d2-7, but k-values of L and W were equivalent from d7-30. Increases in decay rates were then noted from d30-60; W decomposition remained relatively slow ($k = 0.003\ d^{-1}$), whereas that of L was medium ($k = 0.010\ d^{-1}$).

Site N-- Processing coefficients for L and W over 30 d were $k = 0.018\ d^{-1}$ (fast) and $0.006\ d^{-1}$ (medium), respectively. Both treatments displayed a rapid initial mass loss from d0-2, as was described for treatments at SB; $k = 0.080\ d^{-1}$ and $0.072\ d^{-1}$ for L and W respectively. Processing coefficients decreased after d2; however, L k-values remained relatively high (0.012 and 0.014 d^{-1}; fast), whereas W experienced much slower processing rates (0.0002 d^{-1} and 0.002 d^{-1}; slow).

D. Site effects (mass loss)

L and W decomposed more rapidly at the downstream site (N). Differences in percent mass loss between sites became greater with time, but were not significantly different until after the first week, by d30 ($p = 0.004$ and 0.009, respectively); however, mass loss was significantly greater for LN than LSB by d7 ($p = 0.001$) and remained significantly greater by d30 ($p < 0.001$). By d30, percent mass loss was similar between LSB and WN ($p = 0.760$); given that leaves decompose much more rapidly than wood, this emphasizes the faster decomposition rates of cottonwood at N. Decomposition of cottonwood at SB appeared to lag approximately one month behind those at N in terms of percent mass loss; LSB60 (43%), LN30 (42 ± 7%), WSB60 (21 ± 1%), and WN30 (17 ± 1%).

2.2.2. *Accumulated Organic Matter and Sand*

A. POM type and composition

CPOM dry mass represented a larger portion of the material that accumulated on the substrates than FPOM (Table 3, Figs. 3 & 4). At SB, CPOM represented 78% (L), 85% (AL), 92% (W), and 93% (AW) of total POM that accumulated on days 2, 7, and 30. At N, CPOM represented 88% (L), 94% (AL), 95% (W), and 91% (AW) of total POM. Much of this CPOM

consisted of macrophytes, grass, roots, and twigs. Less frequently and in smaller abundance, seedpods, leaves, and algae also accumulated on the substrates.

B. Changes through time

Site SB--Accumulated POM dry mass was low for all substrates by d2. By d7, these accumulations were 6-16 times greater on W, AW, and AL. W accumulated only a slightly greater amount of POM than AW (11.30 vs. 9.78 g). AL accumulated four times the amount as L; however, values were low (1.64 and 0.40 g). By d30, POM was reduced to values similar to that of d2, but with a larger proportion of FPOM.

Site N--POM accumulations on substrates were 3-11 times greater on d7 than on d2. By d30: 1) FPOM on substrates was in greater proportion, 2) POM was greatly reduced on all treatments, and on L had decreased to an amount lower than it had been on d2, and 3) several substrates were partially or fully buried. The amount of sand collected with the substrates is indicative of the extent of burial. Dry mass of the sand was obtained since burial should affect decomposition and macroinvertebrate colonization.

The reduction of POM by d30 on all substrates appeared to be due to increased water releases from the reservoir (St. Francis Case Lake) above Fort Randall Dam. Although water velocity was not greater at the time of measurement, large fluctuations in water depth and velocity were occurring. This caused movement of the channel at SB (substrates were at times subjected to deeper water and stronger currents), and deposition of sediments at N (substrates were subjected to burial, as indicated by dry mass of accumulated sand).

C. Differences among sites

POM accumulations were substantially greater in mass and diversity on substrates at N than at SB. At SB, with the exception of wood (W, AW) on d7, individual substrates accumulated <1 g of POM. LN accumulated > 8 times the amount of POM as LSB, and WN

accumulated almost 4 times the POM as WSB.

D. Differences among substrates

Site SB--By d2, W accumulated more than twice the POM mass as other substrates. Comparisons of the total accumulated POM over time (r = 9) resulted in similar dry mass between L (1.60 g) and AL (2.15 g), and between W (14.01 g) and AW (11.86 g). W exhibited the potential to accumulate almost nine times the amount of POM as L.

Site N—AL (22.77 g) accumulated a larger amount of POM than L (13.47 g), and W (52.20 g) accumulated more than AW (36.54 g). This was not a consistent pattern throughout the study, but rather was a reflection of material accumulated on d7. W exhibited the potential to accumulate up to 4 times the amount of POM as L. Percent of POM remaining on substrates by d30 (% of d7 POM) was proportional to the extent of substrate burial (accumulated sand dry mass), and occurred in the order AW > L > AL > W (Fig. 4).

2.2.3. *Other material collected from substrates*

Other material removed from the substrates, but not included in the prior measurements, may give further insight into the substrate environments, the use of the substrates by invertebrates (and possibly minnows), and additional food resources.

SB substrates--Chironomid eggs were relatively common on W, AW, and L (d30). They were also noted, but less common, on AL (d30), and AW and W (d60). Oligochaete eggs were collected from W (d60), where they were relatively common, and from AW, AL, and L (d60), in lesser abundance. Cladoceran ephippia were rare but noted on AW and W (d7).

N substrates—Chironomid eggs were rarely encountered on AL (d2, d30). Oligochaete eggs were more common, especially from AW and W (d7), and were also noted on AL and L (d30). Ephippia were rare but encountered on AW (d2, d7). Pieces of insect exoskeleton were noted on AL and AW (d7), and were abundant from substrates that had become buried (d30; L,

AL, and especially AW). Fish scales were collected from AL and W (d2), and W and AW (d30; 5 scales from AW). Duckweed was rare on AW and W (d30).

2.2.4. *Invertebrate Colonization*

Over 60 d, 15,358 invertebrates were collected (*sans* one unpreserved sample). The most abundant taxa were Chironomidae (44%), zooplankton (30%), Oligochaeta (11%), and Trichoptera (8%). The two most diverse groups were Diptera (66 taxa) and Trichoptera (11 taxa). As expected, a large portion of the taxa belonged to Chironomidae (58 taxa).

Several generalizations regarding invertebrate colonization and the effect of site location could be made by comparing total individuals collected from all treatments on d2-30 (n = 36 replicates; Table 4). A total of 110 taxa were identified by d30, and an additional five species were found at SB on d60 (Table 5). Although species richness appears relatively high, many of these species were rare, sometimes accounting for only one individual found from both sites.

(1) Chironomids, zooplankton, oligochaetes, trichopterans, and *Hydra* were most abundant on SB substrates, and comprised 99% of the community. The pattern remained similar on d60; however, simuliids not previously collected on d2-30 had colonized substrates and *Hydra* abundance had increased. Other than *Hydra*, these taxa were also common on N substrates along with ephemeropterans, and to a lesser extent, simuliids, amphipods, isopods, and plecopterans, all of which were more abundant at site N.

(2a) The most abundant taxa collected on all substrates at both sites, were chironomids, zooplankton (primarily Copepoda), and oligochaetes. Fifty-four Chironomidae species were identified from d2-30. Four additional species were identified from SB on d60. In addition, one sample from AWN was not preserved and shows, at least under certain conditions, the high potential for oligochaete reproduction and biomass. After approximately one month in an

enclosed plastic container, 421 oligochaetes were counted. Most of these oligochaetes were living and much larger and longer than those from preserved samples. In addition, 46 live oligochaete egg capsules were noted.

(2b) Chironomidae communities

Site SB--The dominant tribe of all treatments at SB was Orthodcladiini/Metriocnemini (94-100%) of the subfamily Orthocladiinae. *Cricotopus bicinctus* was the dominant species representing 70-92% of chironomid communities, depending on substrate type and day. *C. tremulus* (2-20%) was the next most abundant species, and appeared to be inversely proportional to *C. bicinctus* through time.

Site N--Patterns of species richness followed patterns of chironomid abundance. The dominant subfamily in all treatments was Chironominae. Chironominae represented 52-76% of the chironomids on d2 and d7, and increased by d30 to 83-100%. This appeared to correlate with extent of burial (or accumulated dry mass of sand). *Paratanytarsus* sp. dominated all treatments on days 2 (30-38%) and 7 (9-25%), and W on d30 (35%). *Micropsectra* sp., was the next most abundant chironomid on days 2 (9-14%) and 7(16-38%), and represented 11% on W30. These two genera appeared to be inversely proportional. On d30, *Paratendipes* dominated the other substrates which were experiencing high sedimentation.

(3) Trichoptera was also relatively abundant and diverse. Ten species were found over 30 d, and one additional species was found from SB60. Visual observation indicated that this order represented, at times, a larger biomass than the taxa noted above. At SB, Hydropsychidae (*Hydropsyche orris* and *Potamyia flava*) and Polycentropodidae (*Neureclipsis* sp.) dominated Trichoptera. At N, Hydropsychidae (*H. orris*) and Leptoceridae (*Nectopsyche* sp.) were the dominant trichopterans.

(4) Ephemeroptera (almost exclusively Heptageniidae, *Caenis*, and *Baetis*) were also abundant at N; however, they were typically early instars representing a much smaller biomass. Heptageniidae mature enough to be identified were *Stenonema* sp.

(5) Simuliidae (*Simulium meridionale*), Amphipoda (*Hyallela azteca*), Isopoda (*Asellus* sp.), and Plecoptera (*Isoperla* sp.) occurred in relatively large numbers at N; however, relative abundances of these taxa were low.

(6) Collembola, Coleoptera, and Hemiptera were low in abundance and similar between sites.

Effects of accumulated POM and sand on invertebrate abundance is illustrated in figures 5 (site SB) and 6 (site N) and includes data for each substrate type over time.

ANOVA and Biotic Index Results (invertebrate colonization)

Statistical results for abundance were dependent upon the taxonomic level investigated. Many taxa coincided with significant differences at the family level; however, some taxa within a family exhibited significant differences although the family did not. In general, abundances were highly variable resulting in non-significant differences. Significant differences for the four most abundant taxa; Chironomidae, zooplankton, Oligochaeta, and Trichoptera are illustrated in Figures 7-10. The total remaining taxa are illustrated in Fig. 11. Effects of substrate, site, and time are discussed in the following sections.

Biotic index (BI) values derived from invertebrates colonizing the substrates are presented since they appeared to be correlated with time, site and substrate condition (Fig. 12). Tolerance values in the range of 1-10 were used to rate species, with 1 indicating the most sensitive.

A. Substrate effects

Abundance—Overall abundance indicated that W supported a greater number of

invertebrates in most taxa. Exceptions occurred at SB and included: 1) Chironomidae (Chiron) and Trichoptera (Trich), which were similarly abundant on AW, and 2) zooplankton (Zoo) which were most abundant on L.

ANOVA results indicated that substrate stability may have been the primary factor determining invertebrate abundance, and that organic substrates further contributed at site N. Many of the taxa were significantly more abundant on wood treatments (W and/or AW) and on at least one sampling date and site these included: total invertebrates, Chiron, Trich [Hydropsychidae (*H. orris*) and Polycentropodidae (*Neureclipsis*)], Ephemeroptera (*Baetis, Caenis*, and Heptageniidae), other Diptera (excluding Chiron), and oligochaetes (Oligo). At site N, total invertebrates (Inv) and Chiron were additionally more abundant on the organic wood (W), which coincides with greater POM accumulation and less susceptibility to the accumulation of sediments; whereas, Oligo were more abundant on inorganic wood (AW). In contrast, Chiron at SB were more abundant on AW, along with *Hydra*.

Leaf substrates (L and/or AL) supported a significantly greater abundance of Collembola and Zoo on at least one sampling date and site. Zoo were additionally greater on inorganic leaves (AL vs. L) along with Trich (total Polycentropodidae); whereas, Oligo were more abundant on organic leaves (L vs. AL).

Relative Abundance—At SB: 1) relative abundances of Chiron, Oligo, and Zoo were similar between W and AW, and between L and AL, 2) wood treatments supported a greater percentage of Chiron and Oligo, 3) leaf treatments supported greater Zoo, and 4) Trich was low and similar among all treatments. At N, AL resulted in the greatest relative abundance of Zoo, and L had the greatest relative abundance of Oligo.

Species richness (Fig. 13)—W supported the highest species richness at both sites. On d2-30, WSB supported 7-13 more species than other treatments, and WN supported 15-20 more. At N, W supported 9-13 more species of Chiron than other treatments. Trich species richness

was highest on wood treatments (AW at SB, and W at N). WN also contained the greatest number of Ephemeroptera (Ephem) species.

Biomass--Actual biomass measurements were not taken; however, measures of length and visual cues suggested that invertebrate biomass was smaller on L than other treatments. Most of the taxa from L were on the smaller end of the size range; insect taxa were typically early instars. Larger taxa were typically from W and AW. Since abundance contributes to biomass of these taxa, (1) Trich and Oligo were greatest on wood, (2) Ephem, *Isoperla*, *Hyallela azteca*, and *Asellus* were greatest on WN, and (3) Simuliidae biomass was greater on W.

Biotic Index (BI)—Within sites, WN consistently displayed the lowest mean BI, and WSB had the lowest BI on d2 and d30. The largest BIs resulted from LSB30, LSB60, and LN30. Intolerant species were rare; the only "good water quality" indicator that was somewhat abundant was the ephemeropteran, *Stenonema* with a tolerance value (TV) = 4. *Stenonema* sp. was relatively abundant on wood from N7, representing a mean of 14(8) and 7(1) individuals per substrate. Although rare, taxa with TV ≤ 4 were more abundant on AWSB, AWN, and WN). At N, on d7 two species with TV < 4 were collected; one *Brachycentrus* sp. (Trich) from W with a TV = 1, and one *Odontomesa* sp. (Chiron) each from L and AL with a TV = 2.

B. Time effects (invertebrate colonization)

Abundance—At N, total Invertebrate (Inv) abundance peaked by d7 on all substrates except W, where Inv were most abundant on d30. At SB, Inv peaked by d7 on organic substrates (W and L), and by d60 on inorganic substrates (AW and AL). In general, when Zoo were omitted invertebrates increased in abundance to d7 and decreased by d30; however, invertebrates continued to increase on WN to d30, and increased again on SB treatments by d60. Zoo at N followed a similar pattern; however, at SB they continued to increase to d30 and then decreased by d60.

Overall abundances indicated that dominant taxa varied with time. At SB, Chiron remained the dominant taxa until reservoir releases increased; on day 30 Zoo became dominant (insect taxa decreased and Zoo reached its maximum), and on day 60 Zoo co-dominated with Chiron on L. Results were more variable at N: 1) on d2, dominant taxa included Trich (W and L), Chiron (AW), and Zoo (AL), 2) on d7, dominant taxa included Chiron (AW, W, L), Zoo (AL, W), Ephem (AW) and Oligo (AW), and 3) for d30, see burial effects (below).

ANOVA of abundance-- Increases or decreases in abundance discussed in this section were statistically significant unless stated otherwise.

Day 2--Total invertebrate colonization had structural (W/AW) and organic (W/L) effects on increases in abundance at N, but at SB increased only on L. Chiron were early colonizers of LSB and LN, whereas, early colonizers on WSB and WN included Trich (Hydropsychidae: *H. orris*). Additional increases occurred at N (indications of substrate influencing colonization are noted in parentheses): 1) *Neureclipsis* and Zoo (wood structure); coincided with greater POM accumulation, and cyclopoid copepods experienced a significant increase in Zoo for AW (AW accumulated greater POM than W), 2) Ephem (*Baetis*; organic), 3) *P. flava* (L), and 4) other Diptera (excludes chironomids; W) and Heptageniidae (W).

From d2-7, the only decrease occurred for *H. orris* on WN. POM accumulations increased on substrates and likely contributed to subsequent invertebrate increases. At SB these included 1) Trich (total Hydropsychidae; organic and wood structure), 2) total invertebrates (Inv), *H. orris*, and *Neureclipsis* (organic), 3) Chiron (L), and 4) Plecoptera (Plec)(W; however; Plec increased only on AW at N, hence colonization may have been primarily due to structure with the additional need for an organic substrate at SB due to a comparatively small dry mass in accumulated organic material). Zoo increased on AL, which accumulated greater POM than L. At N, increases on W included: Inv, Oligo, Ephem (*Caenis*), and Amphipoda. LN abundances were not significantly affected at this time.

From d7-30, releases from the reservoir increased and resulted in high water level fluctuation. At SB, in general, insect taxa decreased on all substrates, as did accumulated POM, while non-insect taxa increased on leaf and inorganic substrates. Decreases included 1) Trich [Hydropsychidae (*H. orris*)] (leaf structure and inorganic), 2) Chiron (L), and 3) Polycentropodidae (*Neureclipsis*), Plec (W). Increases included: 1) Collembola (L) and Zoo (leaf structure), and 2) *Hydra* and Isopoda (AW). SB Zoo peaked in abundance, coinciding with significant increases in cyclopoid and calanoid copepods from LSB; whereas increases in ALSB Zoo coincided with significant increases in these copepods, and the cladocerans, *Daphnia* and *Bosmina*. Sediment accumulation and burial of substrates at N contributed to decreases in invertebrate abundance on inorganic substrates, and included: Inv, Oligo, Zoo, Chiron, Ephem (*Baetis*, *Caenis*, Heptageniidae), Polycentropodidae (*Neureclipsis*), Acariformes, Plec, and Amphipoda (Amph). Decreases in Zoo coincided with significant decreases in cyclopoid copepods.

By d60, only substrates from SB were available. These substrates experienced much greater water depth and velocity. In addition, the riverbed had moved and substrates were further from shore. Accumulated POM remained low. On W, Chiron and Oligo increased, whereas *Neureclipsis* decreased. Only one L substrate was recovered, and so although not significant, Chiron increased and Zoo decreased. At N, substrates were deeply buried in sediments and irretrievable.

Species richness—Species richness followed a similar pattern as abundance and was greatest on d7 for W, L, and AL at both sites. On AW, at SB, species richness increased over time and peaked on d60; in contrast, at N, richness peaked on d2 and decreased over time.

Biotic index—Overall, at each site, results suggested fairly poor water quality on d2 and d7, and poor water quality on d30 and d60. At N, organic substrates apparently provided a more favorable environment for intolerant communities on d2; however L was considered "poor" by

d7. SB treatments were more similar until d60, when the organic substrates were considered "poor" and thus the least favorable to intolerant species. Although rare, most intolerant species (i.e. TV ≤ 4) were collected on d7.

Burial effects—Burial of substrates affected colonization on d30 at N. Accumulated sand (dry mass in g) indicated that extent of burial was AW > L > AL > W. This caused abundance to decrease on all substrates except W, which increased and reached its maximum. Sedimentation at this site may have also caused the Zoo decrease by d30 and the obvious change in relative abundances of various taxa. For example, several taxa were similarly dominant on W and included simuliids, *Asellus*, and *Hyallela azteca*. Chiron and Oligo dominated the other substrates, which experienced greater burial. Not surprisingly, biotic indices appeared to correlate with extent of burial: AW (very poor) > L (very poor) > AL (poor) > W (fairly poor). Results also indicate that sedimentation, at N, may have affected colonization as early as d7 for AW and L.

C. Site effects (invertebrate colonization)

Abundance—Comparisons of overall abundance on d2-30 between sites indicate that SB substrates supported greater Chiron, Trich, Oligo, *Hydra*, and Zoo; whereas, N substrates supported greater Ephem, Simuliidae, Plec, Amph, and Isopoda (Iso).

ANOVA results indicated that variations occurred between sampling periods and substrate types. On d7 and/or d30 invertebrates were greater at SB versus N for Inv and Chiron (L, AL, AW), Zoo (L, AL), Trich (L, AW), Hydropsychidae and *H. orris* (L, AW, W), *Pf* (AW), Polycentropodidae (L, W, AW), *Neureclipsis* (all substrates), Collembola (L), and *Hydra* (AW). In general, this coincided with sediment accumulation and burial of substrates at N. Invertebrates occurring in greater abundances at N versus SB occurred on d2 and/or d7 and included Ephem (L, W, AW), *Caenis* and Heptageniidae/*Stenonema* (W, AW), *Baetis* (W, AW, L), *Nectopsyche* (W, AL), other Dip (excludes Chiron; W), Amph (AW), and Acariformes (AL). Oligo were greater at

N (W) on d2, but became greater at SB (AW) on d30 due to burial effects at N. Similarly, Iso was greater at N (AL) on d7, but became greater at SB (AW) on d30.

Relative Abundance—Results of overall relative abundance were similar to taxon abundance results, with the exceptions of Trich and Oligo, which were greater from N substrates; however, on SB substrates (d60) these same taxa became greater than or equal to those experienced at N (d2-30). In addition, percentage Zoo on SB60 substrates were greatly reduced and lower than N substrates on d2-30.

Species Richness (Table 5)--Comparisons of samples collected on d2-30 (n = 36) indicated that species richness at N (102) was almost twice that of SB (52). Comparisons between Chiron communities were particularly dramatic; Chiron abundance was greater on SB substrates (4530 individuals; 46%) than on N substrates (492; 20%), yet species richness was greater from substrates at site N (51) than SB (19).

A greater number of species within "total other Diptera" (excludes Chiron) were also collected from N (7) versus SB (3).

Biotic index— Site N appeared to support more environmentally sensitive species, and BIs were more greatly influenced by substrate type at this site. Average values were consistently lower on N substrates by d2, indicating that a more sensitive community was supported at N; however, by d7 BI values were more similar between sites, and although W continued to support a more sensitive community at N, the opposite occurred for L, with lower values at SB. L and AW values were lower at SB by d30, likely due to substrate burial at N.

Burial effects—Significantly lower abundances of the following taxa occurred on N versus SB substrates: 1) Collembola on L, 2) Zoo on L and AL, and 3) total other insects (excludes Chiron), Oligo, and total other non-insecta on AW. In addition, species richness on AWN and LN decreased to values below those at SB, while their BI values increased beyond those at SB, indicating that only more tolerant communities were supported with increased

sediment accumulation.

2.2.5. *Invertebrate Diets*

At SB, *Cricotopus* spp. (mainly *C. bicinctus* and *C. tremulus*) comprised the large majority of Chiron that contained the following gut contents. At N, *Paratanytarsus* and *Micropsectra* were the primary Chiron that contained these contents; with the exception of animal material. The primary trichopterans were *H. orris*, *P. flava*, and *Neureclipsis* at SB, and *H. orris*, *Nectopsyche*, and *Neureclipsis* at site N.

Cottonwood (cw) material was low in abundance (1-3 particulates), and small (typically much smaller than 1 mm). It was not possible to determine whether this material originated from the treatments; much of it may have been consumed as FPOM. The primary trichopteran consumers of cw were *H. orris*, *P. flava*, and *Neureclipsis* at SB, and *H. orris* and *Neureclipsis* at N.

Biofilm and FPOM--Globular/gelatinous material, which included fungi, was common on substrates. Amorphous material that was not gelatinous in appearance was categorized as FPOM. FPOM was the most commonly encountered gut content in essentially all larvae, and typically a main component for all treatments. FPOM and biofilm were stained to various extents, which typically appeared to be correlated with substrate type. Darker (stained) FPOM was likely due to leachates derived from the organic substrates, i.e. through flocculation of leachates, or adsorption of leachates by accumulated FPOM. In addition, greater abundances of fungi in biofilm from larvae of organic substrates were noted and may have contributed to the darker color. Thus, it appears that the organic substrates were contributing indirectly to invertebrate diets. Additionally, in Trich, the quantity of FPOM and extent of staining were influenced by the taxon. FPOM was a main component in hydropsychids, and FPOM and biofilm were typically lighter in color in *P. flava* The 3% of Hydropsychidae from W that did not contain biofilm were *P. flava*

larvae. Biofilm in Polycentropodidae was similar in quantity and color for all treatments. *Hydroptila* contained only a small quantity of FPOM. Biofilm was typically darker and in larger quantity in *Hydropsyche* spp. and Leptoceridae.

Diatoms were typically pennate, but greater diversity and abundance were encountered in SB Chiron. In general, at SB smaller chironomids had a greater proportion of ingested diatoms. Many early instar Chiron contained diatoms almost exclusively indicating selective feeding. *H. orris* and *P. flava* at SB were the dominant trichopterans containing diatoms. Diatoms were not commonly encountered in larvae at N.

Fiber appeared to be minute plant fibers that accumulated on substrates (i.e root hairs). Many were less than 1mm, and so could be added to the FPOM category. They were similar in appearance among all treatments within a site, and few (i.e. 1-3) were noted in SB larvae. Upon thorough examination, some of the "fibers" appeared to be filamentous algae. Time effects for fiber may have been indicative of changes over time in the periphyton community. Other fiber was likely from detritus accumulated from drift. The primary trichopteran consumers of fiber were *H. orris* and *P. flava* at SB, and *H. orris* and *Nectopsyche* at N. Results for fiber were variable, likely due to a category that was too general and of various origins.

Other vegetation, encountered only in Trich, mainly Hydropsychidae, appeared to be that which accumulated on substrates (i.e. macrophytes and grass). This plant material was larger than "fiber" and similar in appearance among all treatments within a site.

Animal material was almost exclusively early instar chironomids in Chiron. *Cricotopus* spp. at SB, and Tanypodinae (primarily *Thienemannimyia*) were the dominant Chiron larvae with animal material. Zoo (Copepoda) was the most common animal material in Trich at both sites, and was most frequently encountered and abundant in *Neureclipsis*, followed by Hydropsychidae.

Inorganic particulates (i.e. sand grains) were commonly encountered, and a main component in SB larvae. Chiron and many of the Trich of both sites often contained sand in

equal proportion to FPOM; however, there were exceptions, and *Hydropsyche spp*, contained a smaller proportion of sand than other trichopteran taxa.

Other—Desmids were not common, but encountered in SB Chiron, almost exclusively *Cricotopus* spp., and in SB Trich, mainly *H. orris*, *H. simulans*, and Hydroptilidae. Seeds were even less common but encountered in *H. orris* at N.

Trophic Relationships (Functional Feeding Groups; FFG)

Values represent the maximum percent of individuals within each FFG; many taxa were placed in more than one group. Fig. 14 illustrates the proportion of various taxa within each FFG. It should be noted that many of the larvae were early instars and so likely functioned as collectors; therefore actual values for many of the other FFGs are likely overestimated. Collectors were the most prevalent FFG. The majority of the invertebrates collected from SB and N substrates were collector-gatherers (CG), up to 55% and 57%, respectively. If Zoo were excluded as in many investigations, CG represents up to 89% and 73% of the invertebrates, respectively. Shredder-herbivores (SHH) were abundant at SB due to a preponderance of Chiron in the genus *Cricotopus*, which function as CG/SHH. Zoo was included in this study, because they appear to be utilizing substrates and they serve as a food source for macroinvertebrates and fish. Predators and collector-filterers (CF) were the next most abundant taxa. Results for Inv with and without Zoo were compared. Comparisons were considered when their differences were $\geq$ 10%. It is evident that Fig. 14 may be misleading and represents the potential feeding habits of the macroinvertebrate community only. When zooplankton are considered part of the community, and gut content analysis is taken into consideration (e.g. *Cricotopus* was not functioning as an SHH, and predatory habits of zooplankton appeared insignificant), CG, CF, and SHH become more similar between sites. Thus, feeding habits of the communites were very similar between sites, with the exception of the greater scraper groups at N.

Amph, Iso, and Physidae may function as shredders of detritus (SHD), as feeding

behaviors may lead to particle size reduction; however, this did not appear to be the case in this study. In addition, these taxa were not common: *H. azteca* and *Asellus*, at N, represented 4% and 3% of the total population, respectively; these same taxa represented <1% at SB, as did *Physa* at both sites. The chironomid, *Paratanytarsus*, was relatively common at N, but was not included in these results due to its unknown FFG. The presence of *Paratanytarsus* would affect Inv on LN and WN communities by 4% & 5%, respectively, and chironomid communities would be affected by 15% and 29% on LN and WN. Comparisons of *Paratanytarsus* and *Micropsectra* colonization and gut contents suggested that their FFG may be similar (CG feeding mode); thus adding *Paratanytarsus* may have further increased the abundance and relative abundance of CGs.

A. Substrate effects

Diet (Figs. 15 & 16); all ANOVA differences discussed in this section were significant

Chironomids— Few differences were significant. Substrate structure was an important factor in gut contents on d7, as indicated by more frequently encountered larvae with biofilm from SB wood substrates (W, AW) and diatoms from WN versus LN. Cottonwood in larvae from SB30 was more frequently encountered from W than AW.

Trichoptera—Specific gut contents were never encountered more frequently in WSB than AWSB, nor in LN than ALN; however, a greater percentage of larvae from W than L had biofilm at both sites by d7. Gut contents more frequently encountered in larvae from wood than their leaf counterparts, suggesting substrate structure effects, included: 1) biofilm in larvae from WSB7, WN7, and AWSB60, 2) cottonwood in larvae from AWSB7, and 3) fiber and other vegetation in larvae from AWN7). Contents more common in larvae from organic substrates than their inorganic counterparts occurred on d7, and included: 1) biofilm and fiber from WN, and 2) cottonwood from LSB. In contrast, contents more common in larvae from inorganic substrates included fiber from ALN2 and cottonwood and diatoms from AWSB7.

Additional observations:

Cottonwood (cw)— *Stenonema* sp. from WN, was the only Ephem to contain cw.

Biofilm—Although ALSB Trich more frequently contained biofilm on d2 than AWSB, the opposite resulted when data were combined for d2-30. The combined data also resulted in more similar results between LN and WN. In larvae from organic substrates, biofilm was in greater quantity, darker in color, and contained more fungi. At SB on d2 and d7, the exceptions to pale (unstained) biofilm in Chiron guts occurred in *Cryptochironomous* (n=1) and *Micropsectra* (n=1) from organic leaves (LSB). The only exception to stained biofilm in Chiron guts on d30 was from inorganic leaves (ALSB).

FPOM—At both sites, FPOM was typically darker in larvae from organic substrates. FPOM from WSB Chiron was typically darker in color than those from AWSB. In Chiron of WSB2, FPOM was darkly stained in larvae from one of three samples, in which a large abundance of larvae existed. The other WSB2 replicates had few Chiron that contained unstained FPOM. FPOM in Chiron of AWSB was mainly unstained. At N, FPOM was typically stained for all treatments; however, it was darkest in larvae from W. In general, at N, when little FPOM was present in guts it was not stained, but when stained FPOM was present it occurred in larger quantities.

Diatoms appeared to be ingested by a greater percent of larvae from wood and inorganic substrates. WSB2 Chiron from one of three samples contained an abundance of larvae with a large abundance of diatoms. Other WSB2 samples contained fewer Chiron that contained fewer diatoms. Diatoms were a main gut content in ALSB2 Chiron, but few diatoms were encountered in those of LSB2. Diatoms in *Hydroptila* spp. were encountered on d60 only, and in few larvae; however one larva from WSB60 contained more than 17 diatoms.

Animal material—Overall, d2-30 combined, animal material was more common in N Trich from leaf treatments. In contrast, animal material in ALSB Trich was uncommon;

however, by d60 at SB, animal material was most common in Trich from W and AL.

Functional feeding group (substrate effects)

Data from days 2, 7, and 30 were combined, and abundance and maximum relative abundance of invertebrates within specific FFGs were analyzed.

Abundance (Figs. 17 & 18)

SB—Abundances of CG and SHH were greatest on wood (W/AW) indicating structural effects, and scrapers (Scr) were somewhat greater on W. Predators (Pred) were greatest on L; however, when Zoo were omitted Pred and CF were also greatest on wood.

N—Abundances were greatest on W for CF, CG, SHH, Pred, and Scr; whereas they were least on L for CF, SHH, and especially CG and Scr. This pattern remained the same when Zoo were omitted from the analysis.

Relative abundance (%; Figs. 19 & 20)

SB--Substrate structure was an important factor for differences in relative abundances of FFGs (Fig.19). CG and SHH were greater on wood (W/AW) than leaf (L/AL) substrates; CG by 40% and 38%, SHH by 30 and 33%. In contrast, CF and Pred were greater on leaf substrates; CF by 12% and 16%, Pred by 28% and 23%. However, if Zoo were excluded results become similar (differences are < 10%).

N—Relative abundances of FFGs were similar among substrates (Fig.19); however, with Zoo omitted (Fig. 20a), differences indicated that: 1) Scr made up a smaller proportion on L than other substrates; i.e. 12% less on L than W due to a smaller relative abundance of Ephem (*Caenis* and Heptageniidae) on L, and 2) CF were greater on W than L by 9% due to greater Chiron and Simuliidae on W. CF Zoo was greater on L than other substrates (Fig. 20b). Within Chiron, CG were greatest on inorganic and leaf substrates, CF were greatest on wood, and Pred were greatest on organic (Fig. 20c). Within Trich, CF was greatest on organic substrates, SHH were greatest on inorganic, and CG was greatest on AL (Fig. 20d).

B. Site effects

Diet (Figs. 15 & 16)

ANOVA results--All differences discussed are statistically significant. No site effects occurred on d30 when substrates at N were buried, thus the following are results from d2 and/or d7.

Chiron—A greater percent of larvae at N contained cw (AW), fiber (wood; W/AW), and biofilm (all treatments), whereas at SB, diatoms were encountered in a greater percent of larvae from all treatments.

Trich—A greater percent of Trich at N contained fiber (L) and other vegetation (L, W, AW), whereas a greater percent of SB larvae contained diatoms (L, AW).

Additional observations:

Diatoms—At SB, many early instar Chiron guts contained almost exclusively diatoms, and a larger diversity and abundance of diatoms were encountered. In contrast, at N, few diatoms were encountered in < 10% of Chiron, overall, from all treatments. Hydropsychids were the primary Trich consumers of diatoms at SB. In contrast, N Trich contained essentially no diatoms.

Biofilm and FPOM—Biofilm from N invertebrates was more darkly stained and contained a larger quantity of fungi. Similarly, FPOM in larvae was typically darker in color at N than SB.

Fiber—Fiber was relatively common in N Oligo from all treatments; however, no fibers were noted in those from SB.

Other vegetation--In SB Trich, this material was in small quantity and appeared to be mainly grass. Trich from N contained a larger quantity and diversity of plant material than those of SB and included macrophytes; however, the quantity was variable in all treatments of N from few to being the main component in some guts. Rarely, seeds were noted in *H. orris* at N,

exclusively.

Animal material—Differences were not significant; however, Trich from N7 and N30 contained eggs (likely from Chiron and Oligo). Eggs were less frequently encountered and less abundant than Zoo and Chiron in Trich guts.

Functional feeding group (site effects)

Abundance (Fig. 17, 18)

Abundances of most FFGs were greatest on SB substrates, with the exception of Scr, which was greatest on those of N; however, when Zoo was omitted, CF abundances were similar between WSB and WN.

Relative abundance (%; Figs. 19, 20, 21)

Site effects on FFGs were more pronounced on leaf substrates. Overall, the greatest FFGs to be affected by site were SHH and Scr (Fig. 21 a & b).

Percentage FFGs were greater from SB substrates for: 1) CF from LSB by 10% and ALSB by 21%; however, when Zoo is omitted results are similar between sites, 2) SHH from all substrates, 17-19% greater on leaf and 47-51% greater on wood; when Zoo is omitted differences became even greater at SB than N (63-69%), and 3) Pred from LSB by 14%; when Zoo were omitted, Pred was more similar between sites.

Percentage FFGs were greater from N substrates for: 1) CG from LN and ALN by 29% and 25%; however, when Zoo were omitted differences are < 10%, and 2) Scr from all substrates by 8-15%, and with Zoo omitted, by 7% on LN and by 18-19% for the other substrates.

Scr represented less than 1% of the community at SB but 14% at N. SHH had the potential to be high at SB due to the preponderance of the Chiron, *C. bicinctus*, which may have functioned as SHH in the late instar; however, a more diverse assemblage of invertebrates at N had the potential to function as SHH. Within Chiron, CG and SHH were greater at SB; whereas,

CF and Pred were greater at N. In contrast, within Trich, CF and Pred were greater at SB; whereas CG were greater at N (Fig 21c,d).

C. Time effects

Diet

Chiron--Diets of Chiron were significantly affected by time only at SB. Significant increases in the proportion of larvae with specific contents included: 1) d2-7; increases in larvae with fiber from leaf (L/AL), biofilm from wood (W/AW), and diatoms from L, 2) d7-30; increases in biofilm from leaf (L/AL), and decreases in larvae with diatoms from all substrates, and 3) d30-60; W larvae displayed increases in animal material and decreases in cw and desmids.

Trichoptera—At SB, significant effects occurred on L and included increases in fiber by d7, decreases in fiber and diatoms by d30, and decreases in biofilm by d60. Trich at N resulted in decreases by d7 and included fiber from inorganic substrates (AW/AL), and biofilm from L.

Additional observations:

Biofilm in Chiron—Ingested biofilm became darker with time, more slowly from ALSB, and occurred in greater quantity in larvae from wood treatments. At N, biofilm was a main component and stained in WN Chiron throughout time, but did not become a dominant component in other N treatments until d7. By d30 biofilm was a dominant component only in Chiron from wood treatments, and biofilm from AWN larvae became more darkly stained, similar to the organic treatments. Ingested biofilm became darker with time for all treatments.

FPOM in N invertebrates and in WSB Chiron typically became darker with time.

Diatoms—At SB, the percentage of Chiron with diatoms, and abundance and diversity of diatoms ingested peaked on d7 and became the main gut content in some larvae; however, the percentage of Chiron with diatoms significantly decreased by d30, and abundance and diversity

of diatoms dramatically decreased.

Fiber—A larger percentage of SB Chiron ingested fiber when accumulated FPOM had increased on substrates, as on L7, AL7, and AW30. The percentage of LSB Trich with fiber and the amount of POM accumulated on the substrates followed the same pattern (d7 & d30). At N, by d7, Trich from inorganic substrates consumed less fiber with increased POM accumulation.

Other—The decrease in vegetation (AW) from d30-60 coincided with an increased current velocity and depth, which adversely affected POM accumulation.

Functional feeding group (time effects)

Abundance

SB—From d2-7, increases occurred in CF, CG, SHH, and Pred on all substrates. From d7-30: 1) increases included CF and Pred on all substrates; however when Zoo were omitted CF and Pred decreased on all substrates, and 2) CG and SHH decreased on all. From d30-60: 1) CG and SHH increased on all substrates but L, and 2) CF and Pred decreased on all; however when Zoo were omitted CF and Pred decreased only on L and increased on the other substrates (wood, inorganic), and 4) CG and SHH decreased on L.

N—From d2-7, increases occurred in: 1) CG, SHH, Pred, and Scr on W, L, AL (organic, leaf), and 2) CF decreased on W, AW, L (wood and organic). From d7-30: 1) CF and CG increased on W, 2) SHH and Pred decreased on all, and 3) CF, CG, and Scr decreased on all but W.

Relative abundance

SB—From d2-7 (when Zoo were omitted), a decrease in SHH was noted on wood (W/AW) by 15% and 10%. From d7-30: 1) CG increased on wood and organic, W, AW by 12-19% (W, AW, L), 2) SHH increased and CF decreased on L by 10% each, and 3) when Zoo were

omitted, differences in FFG were generally less than 10%; however, SHH decreased on L by 17%. From d30-60: 1) CG and SHH increased on all by 35-63%, and 23-44%, respectively, 2) Pred decreased on all by 28-49%, 3) CF decreased on W by 10%, and 4) when Zoo was omitted, these differences were not as great; CG and SHH increased on L by 11% and 24%, CF decreased on L by 10%, and SHH decreased on W by 11%.

By d2 (excluding Zoo), FFGs followed the pattern CG ≈ SHH > CF > Pred > Scr (exception; AL CG > SHH). This pattern remained similar on d7, d30, and d60, except CG became greater than SHH on all substrates. FFGs of Zoo indicated that CF taxa dominated organic treatments, whereas Zoo Pred dominated the inorganic treatments. By d7, within Zoo, CF were greater than Pred for all substrates except AL; however, Pred dominated by d30 when Zoo were most abundant.

N—From d2-7: 1) CG increased on all by 13-20%, and 2) CF decreased on all by 13-30%; when Zoo were omitted CF decreased only on organic and wood (not AL). From d7-30: 1) CG increased on wood by 10%, 2) Pred decreased on W by 23%, and 3) when Zoo was omitted SHH decreased on AL/AW by 13%, Scr decreased by 5-26%, and CG increased on L by 14%.

By d2, excluding Zoo, CG > CF > Scr > Pred ≥ SHH (exception; L Scr ≈ SHH). CF comprised a greater percentage of the community on organic treatments. By d7, percentages of Scr reached their maximum but were comparatively low on L; 21-26% versus 10% for L. Scr became greater than CF for all but L. By d30, Scr percentages reached their minimum. On d30, patterns of FFGs appeared to be dependent on extent of burial. AW and L displayed similar patterns and experienced the greatest extent of burial, whereas W and AL were similar and experienced less burial/sedimentation. As the amount of accumulated sand increased, the percent of: 1) CG and Pred increased, and 2) CF and scrapers decreased. The Zoo community consisted exclusively of Pred on AW30, again demonstrating the effects of burial on the CF community. CG Zoo (nematodes) also decreased in abundance by d30 and was non-existent in treatments

experiencing the greatest burial.

D. Other taxa

Small sub-samples of the following taxa were analyzed: 1) copepods and cladocerans contained FPOM, sand, biofilm, and rarely diatoms, 2) Oligo contained FPOM, sand, biofilm, cw (results were similar to or less than that of the Chiron), and fibers (relatively common in Oligo from N), 3) Plec (*Isoperla*) contained FPOM, sand, and biofilm. Results from the remaining taxa appeared to be within the range of those discussed in this section.

E. Relative dominance of FFGs summarized (Fig. 22)

SB--Omitting Zoo, and taking into consideration the gut content analyses, it appeared that collectors represented up to 99% of both L and W communities; CG represented up to 84% and 91% of L and W, respectively. The preponderance of CGs was largely due to the chironomid *C. bicinctus*, which can also function as a SHH but did not appear to be doing so to a significant degree during this study. Thus, SHH represented only up to 6% and 3% of the community. Pred represented up to 8% and 4%. All other feeding modes represented less than 1%. Within the Zoo community, even the predators contained almost exclusively POM and biofilm; thus adding Zoo to the invertebrate community increased collectors.

N—Overall, the Zoo community at N had little effect over relative abundances of FFGs. With Zoo omitted, collectors represented up to 93% and 98% of the invertebrates on L and W, respectively; CG made up 76% and 72%. The chironomid *Paratanytarsus* was omitted from the FFG data due to its unknown FFG; however, if it was functioning as a CG, then CG would increase by 4% and 5% on L and W. Scrapers represented up to 8% and 20% on L and W, SHH represented up to 11% and 9%, and Pred represented up to 17% and 11%. All other feeding modes represented less than 1%.

2.3. Discussion

2.3.1. *Leaf and Wood Processing*

Leaching (day 0-2)—Leaf packs and wood experienced an initial rapid rate of decay, mass loss was significant, and percent mass loss was similar between substrates and sites (12-15%). This coincides with phase 1 in chapter 1, in which rapid leaching of most soluble substances generally occurs in 1-2 days. Percent mass loss was less than that described by Hill et al. (1992), where cottonwood leaves in prairie streams had a 31% leaching loss after 48 hours. This is likely due to differences in leaching loss before placement in the stream.

Microbial decomposition (day 2-30)--Decay rates became slow for all treatments with the exception of site N leaf packs. Leaf pack decay rates at site N remained relatively fast, and a significant percent mass loss occurred between days 7 and 30. Biofilms were developing on substrates, which have been shown to affect leaf decomposition and provide a food source for detritivores in streams (Maltby 1992, Sobczak 1996). The extent of physical abrasion is unknown; however, although the leaves and wood had become softened and darker in color, they remained intact. In addition, Hill et al. (1992) found a strong correlation between microbial respiration and mass loss for the first 28 d of their study; increased physical weathering associated with higher flow rates was not a primary determinant of leaf breakdown, and microorganisms appeared to cause up to 66% of leaf mass loss. Results of this study for site N leaves were essentially the same, with microorganisms as the likely cause of approximately 64% of leaf mass loss over the first 30 d. *SB day 60*—Decay rates for site SB leaf packs increased from day 30-60 (medium), and since leaves remained intact, further microbial activity was indicated. Although mass loss was significant for site SB wood, decay remained slow. Treatments at site N were deeply buried in the riverbed.

Cw leaves--Overall breakdown rates experienced by leaf packs were more rapid at site N than site SB (fast and intermediate, respectively). Percent mass loss over 30 d resulted in SB

leaves 16(2)% and N leaves 42(7)%. Assuming losses by day 2 were due to leaching, then 4% of SB leaf mass and 27% of N leaf mass was lost due to other factors (i.e microbial activity). During the 14-d microcosm experiment (chapter 1) leaves with invertebrates lost 34(4)% of the initial mass (k = 0.029; fast). This coincides with the field results at site N; mean mass loss of leaf packs from days 7 and 30 was 31% after approximately 12 days (assuming mass loss was linear). Similarly, the mean k-value of these same treatments resulted in k = 0.025 (fast). Only one leaf pack replicate was available by day 60 due to loss of some experimental units at site SB to drift, and burial of treatments at site N. The remaining leaf pack at site SB lost an additional 23% of its mass, resulting in a total loss of 43%.

Gawne (unpub.) observed cottonwood leaf breakdown in four middle Missouri reaches, which included sites SB and N. His 1994 study was also conducted over 60 d in spring/summer. Results indicated a 50% leaf mass loss with k = 0.009 (medium). It is likely that leaf packs at site N (fast) in our study may have experienced an even greater percent mass loss by day 60; however, treatments were irretrievable. Webster and Benfield (1986) indicated that cottonwood leaves had intermediate breakdown rates (k = 0.005). On fourth order intermittent and perennial streams, Hill et al. (1992) observed intermediate (k = 0.007) and fast (k = 0.014) breakdown rates, respectively. Gawne's k-value, which included four sites, was equivalent to our k-value at site SB over 60 d. His larger leaf packs, cages of eight 40-g leaves, likely influenced breakdown rates resulting in lower values. The lower surface area to volume ratio experienced by larger packs results in less exposure to current, thereby slowing microbial degradation and physical breakdown (Gawne, unpub.). Cummins (2002) found that leaves in mesh bags were processed significantly more slowly than those of tethered leaf packs, which coincided with lower colonization of hyphomycete fungi.

Cw Wood--Overall breakdown rates were slow for site SB wood and medium for site N wood; however, decay rates measured after day 2 were always slow. By day 30, SB wood and N

wood lost 13(1)% and 17(1)% of their mass, respectively. Assuming losses by day 2 were due to leaching, then only 1% of SB wood mass and 4% of N wood mass was lost via other factors (e.g. microbial activity). Wood at site SB lost an additional 8% of its mass from day 30 to day 60, indicating further microbial activity since substrates remained intact. There is little information on decay rates for woody debris, but some studies suggest that twigs less than 1 cm in diameter require 0.5 – 1 decades, wood 5-10 cm in diameter require possibly 5 decades, and larger trees require 10-25 decades (Allan, 1995). Thus, wood in this study should require at least a decade to fully decay.

Burial--Gawne's relatively large cages were more susceptible to burial than the tethered leaf packs of this study. He investigated the effects of burial on cottonwood leaf and grass decomposition in microcosms, which mimicked these same field sites. The leaves became black and leathery after 3 d due to anoxic conditions and all material gave off a distinctive sulfurous odor when sampled; however, results indicated that burial had no effect on decomposition rates. Although leaf packs at site N were more susceptible to burial than wood, leaves continued to lose a greater percent of mass by day 30.

Influences of site location--Rates of decay are faster at site N than site SB, likely due to higher microbial activity. Since site differences do not affect leaching of substrates, the higher k-values and somewhat greater mass loss at site N by day 2 may indicate that microbial activity was already contributing to decomposition of leaves and wood at this site. Up to an additional month was required for SB substrates to lose masses similar to those attained by substrates at site N. In addition, leaf packs at site N lost a significantly greater percent of mass than wood by day 7 and again by day 30, whereas at site SB differences in percent mass loss were not significant between leaf packs and wood through day 30. By day 30, SB leaves and N wood lost a similar percentage of mass. Since leaves typically break down at a much greater rate than wood, this exemplifies the influences of site location on breakdown rates.

As stated in chapter 1, Lewis and Clark and Francis Case Lakes, which lie on either side of our study sites, are phosphorus limited, and water entering this reach from reservoirs was nearly devoid of TP and TN (Hesse et al. 1989, Schmulbach et al. 1992). Decomposition of macrophytes at site N in addition to inputs from other sources (i.e. tributaries, wetlands, and backwaters) may have resulted in a higher concentration of nutrients at that site. Greater nutrient concentrations and warmer temperatures at site N favor microbial growth and activity (Tank et al. 1992, Kaushik and Hynes 1971), which in turn aid in the breakdown of organic material. In addition, microbial density and composition may be influenced by inputs from those sources. Although physical abrasion was not obvious, it should have been greater at site N due to higher current velocities and sedimentation, which could increase breakdown rates.

Implications

Mass loss of cottonwood was due to leaching and microbial activity. During the first month, leaf packs at site N were the only treatments to lose a substantial percentage of mass to microbial activity (27%). An additional month was required for leaf packs at site SB to lose the same percentage of mass. Inputs at site SB, if prevented from moving downstream, should be available to invertebrates for a longer period of time since those downstream are more susceptible to burial. However, breakdown rates and thus conditioning of substrates to a more palatable invertebrate food resource are likely to take a longer period of time at site SB than at site N. Although terrestrial inputs are likely to be buried in the river bottom where substrates are not available to many taxa, their ultimate fate is largely unknown. Leaves and wood were still intact and decomposing after two months, burial does not appear to affect decomposition rates in this system, some taxa are specialized in utilizing buried detritus, and buried detritus may be reintroduced multiple times depending on discharge. Thus burial of organic material does not necessarily mean that contributions have become insignificant to the system. However, the dynamics of reservoir releases resulted in large amounts of sediments being deposited at site N.

Sometime after 30 d and by 60 d, substrates became so deeply buried in tightly packed sediments, that despite substantial efforts, we were unable to remove them from the riverbed. Such deep burial should significantly decrease their contribution to higher trophic levels.

2.3.2. *POM and Sand Accumulation*

Comparisons with Other Data

A large proportion of the POM was CPOM on SB wood (92%), N wood (95%), SB leaf packs (78%) and N leaf packs (88%). This is not surprising since transport distances are much shorter for larger material. For example, excluding flood conditions, it has been shown that leaves and small pieces of wood travel less than 10 m before retention or burial, whereas FPOM in large rivers can travel more than 8 km/day (Allan, 1995).

In a 1993 study, Gawne (unpub.) noted a peak in organic matter drift in May as compared to April and October, which he believed corresponded to spring floods. In this study, POM accumulations reached their maximum in May as compared to June and July, when flows were more stable. Gawne concluded that Ponca Creek, just upstream from site N, significantly influenced the amount of material present in the spring when flows in the main channel were low. In his study, leaves, grass, and small pieces of wood dominated material from Ponca. In this study, grass and twigs were dominant components of material that accumulated on substrates, but leaves were less frequently encountered and in small quantity. Roots and macrophytes also dominated the accumulated POM at site N. This plant detritus appeared to be due to local inputs at that site.

The obstruction of water flow by debris dams causes sediments and organic matter to settle in pools formed upstream and creates hotspots of heterotrophic activity (Hedin 1990, Allan 1995). Thus, the experimental substrates (especially wood) may have made further contributions not measured in this study.

Site and Treatment Differences

Substrates as Debris Dams--As expected, the results indicate that wood is a better retention substrate than leaf packs. Overall, wood accumulated approximately nine times more POM than leaf packs at SB, and up to four times that of leaf packs at N. Results were similar but somewhat less dramatic for the artificial substrates.

Expansion of Habitat and Microhabitats--Not only were POM accumulations from the drift substantially greater in mass at site N, but diversity was also higher. Increases in accumulated CPOM, especially on wood from both sites, resulted in habitat expansion (total surface area and microhabitats). Water flow alteration may be one variable contributing to microhabitats, and on a large scale should be more greatly affected by wood.

Alternate Food Resources--Increased CPOM led to a greater abundance and diversity of food resources. In addition, a greater amount of FPOM may be trapped with the CPOM. Detritus from macrophytes was relatively abundant on site N substrates. Grass accumulated on substrates at both sites, but more so at site N. Although grass was neither frequently encountered nor abundant when present, it still may potentially be an important food resource for invertebrates in this system.

Effects of Time, Increased Reservoir Releases, and Burial –Substrates accumulated the largest amount of POM at site N on day 7. Increased reservoir releases by day 30 greatly reduced POM accumulations, and a larger proportion of the remaining POM consisted of FPOM. At this time, several of the substrates at site N were at least partially buried. Burial was much greater for leaf packs versus wood; however, the artificial wood was most susceptible to burial likely due to the fact that it was typically in closer contact with the riverbed. The percent of POM remaining on substrates by day 30 was proportional to the extent of substrate burial (artificial wood > leaf packs > artificial leaf packs > wood). Although buried substrates would be unavailable to many invertebrate taxa and may subject the substrates to anoxic conditions, greater retention of

accumulated POM may offer additional benefits or extend invertebrate utilization of the substrate. Water depth and current velocity had greatly increased by day 60 at site SB, resulting in little POM accumulation. In contrast, vast quantities of sediments were deposited at site N and substrates were subjected to deep burial.

2.3.3. *Invertebrate Colonization*

2.3.3.1. Disturbance

Disturbance has been shown to play a central role in structuring stream communities (Lake 2000). In this study, fluctuation of river discharge by reservoir releases was the primary determinant of invertebrate composition on substrates. This disturbance led to a reduction in invertebrate abundance, species richness, and sensitive species. A study conducted on an impounded Utah river (Wolz and Shiozawa 1995) supports this observation; distribution and abundance of benthic invertebrates in four habitat types were attributed to flow conditions and sediment size, and flow conditions were likely the determining factor.

Reservoir releases resulted in high water level fluctuations and transport of vast amounts of sediments downstream, and cessation of releases led to dewatering factors. Increased releases also correlated with a decrease in accumulated POM on substrates and greater burial. These releases appeared to have similar impacts as a flood (Lake 2000), but were constrained within the channel. The exception to this was noted in a preliminary visit to the field sites. Unlike site SB (upstream), during a high water release, the river flowed over the shallow banks at site N (downstream) into adjacent wetlands and surrounding areas. In this way, resources may be transported into the river; however, the following dewatering event left many animals stranded in pools.

<u>Upstream site (SB)</u>

In flooding streams, large volumes of rapidly moving water exert high shear forces that

suspend sediments, move and redistribute bottom materials, scour and abrade the streambed, remove plants (including microscopic algae), move detritus, snags and debris dams, and kill, maim, and displace biota. Where streams have a loosely structured sand bed and few refugia (like site SB), flood impacts may be great and recovery of macroinvertebrates slow (Lake, 2000).

Increases in zooplankton abundance with increased reservoir releases were noted along with a decrease in the abundance of insect taxa by day 30, likely due to removal by high shear forces. In addition, frequent high water events move small patches of streambed as occurred at site SB. Originally, site SB treatments were placed in near-shore areas; however, channel degradation and increased water depth caused the substrate site to become part of the main channel by day 60 and resulted in the loss of some substrates. Since benthic invertebrates tend to be more abundant at near-shore areas, this relocation of the substrates likely contributed to decreased invertebrate abundances.

As typical of stressed ecosystems, invertebrate abundance was comparatively high, while species richness remained low (Simpson and Bode, 1980). Colonization was dominated by invertebrates that are more tolerant of environmental stresses, e.g., *C. bicinctus* (Orthocladiinae), and hydropsychid caddisflies. According to Simpson and Bode (1980), *C. bicinctus* is a very adaptable, opportunistic, and pollution tolerant species that increases in abundance when stresses eliminate more sensitive species and can become the most abundant organism. The preponderance of *C. bicinctus*, accompanied by low species richness indicates a non-organic stress factor such as alterations in physical factors, i.e. water temperature and flow or the presence of toxic substances (Simpson and Bode, 1980). Site SB was more greatly impacted by cold-water releases from the reservoir and altered flow. Armitage (1977) and Armitage and Blackburn (1990) also reported that benthic invertebrates immediately below a dam, on the Tees River, decreased in species richness, but increased in overall abundance of invertebrates; they also noted an abundance of orthoclad midges and oligochaetes.

Downstream site (N)

High reservoir releases resulted in sediment deposition at site N from upstream sites, reducing water depth. When the releases ceased, treatments were subjected to shallow water and at times were exposed; these effects were greatest at site N. Similarities to drought effects were observed (Lake 2000), such as a reduction in habitat space and the formation of pools, which entrap invertebrates. Other effects may include deterioration of water quality, high water temperatures (a greater increase in temperature was noted at site N), hypoxia, more limited instream transport (of nutrients, organic leachates, and biota) and increased competition and predation (Lake 2000). Any or all of these factors may have contributed to the reduction in invertebrate abundance and diversity on site N substrates.

Sediment deposition also caused burial of several treatments at site N, and all substrates were deeply buried in the riverbed by day 60. As substrates accumulated large amounts of sediment, species composition was affected and abundance and diversity diminished. Burial/high sedimentation has been shown to reduce invertebrate diversity, richness, and total community biomass (Cooper 1987, Wilbur 1974), particularly if the sediments are anoxic (Wilbur 1974). Although species richness was much greater at this site, many of the species were rarely collected, and the more common species are known to be pioneers that are more resilient to environmental stresses. At site N on day 30, the chironomid community increased in the proportion of Chironominae; L (100%), AL (94%), W (83%), and AW (100%). These percentages corresponded to the extent of burial of the substrates. Compared to day 7 values, species richness on day 30 decreased by 42% on WN likely due to sedimentation, and the other substrates experienced greater burial and decreased 70-82%.

Early colonizers

Further emphasizing the effects of disturbance on shaping invertebrate composition on our substrates, several of the more common taxa found in this study are apparently resilient after

disturbance, and expected to be early colonizers of disturbed substrates, i.e. Hydropsychinae caddisflies (*H. orris, P. flava*), Baetidae, Heptageniidae, Simuliidae, opportunistic orthoclads (e.g. *C. bicinctus*), and Chironominae filterers (Mackay 1992).

Simuliidae may be of concern since this family contains many blood-sucking pests that can be disease/parasite vectors (e.g. *S. meridionale*). Simuliids greatly increased when disturbance appeared to be highest, thus disturbance caused by reservoir releases may increase simuliid abundance. Simuliids are known to be early colonizers of disturbed habitat, attaching to recently denuded substrates; they avoid substrates covered with detritus, algae or thick biofilms (Mackay 1992). By day 30, simuliids co-dominated wood at site N. Simuliids at site SB were not collected until day 60, when releases were highest, and were most abundant on wood. In addition, Lake (2000) noted that simuliids appear to be favored by drought conditions. This is further supported by even larger aggregations of simuliids noted on the conduit tether poles at site N on day 60; all treatments at site N were deeply buried and the sediments above them exposed or in shallow water.

Invertebrate tolerance and substrate quality

Invertebrate communities were dominated by tolerant species, whereas intolerant species (i.e. TV ≤ 4) occurred only rarely. Note that these species occurred on day 7 before increased reservoir releases, when accumulated POM was at its maximum and before sedimentation effects increased. This was also after the rapid leaching of leaf pack and wood substrates and during the slow rate of decay of these substrates; except for site N leaf packs, where they remained relatively high. Site N appeared to support more environmentally sensitive species, and biotic index values indicated that a more sensitive community was supported at site N by day 2.

Overall, biotic index and tolerance values indicated that wood supported more environmentally sensitive communities than leaf packs and artificial substrates, and leaf packs did not support taxa as sensitive by day 30. In general, fewer intolerant invertebrates were supported

by day 30, indicating increased environmental stress. Results from site N indicated that organic substrates supported more of these taxa by day 2 and that sediment accumulation was the primary factor reducing the suitability of substrates. In addition, the reduction in these taxa on leaf packs by day 7 may coincide with faster leaf breakdown rates. At site SB, treatments were more similar until day 60 when organic substrates were the least favorable to intolerant species, and thus may be an indication of over-conditioning of the substrates, rendering them less suitable for sensitive taxa. Increased water releases from the reservoir resulted in increased water depth and velocity at site SB, which likely further reduced the presence of sensitive taxa on substrates.

2.3.3.2. Habitats & Habits

Differences in site and substrate characteristics also affected invertebrate colonization. Merritt and Cummins (1996) described insect habitats and habits that offer further insight into these results.

Upstream site (SB)

The river at site SB is controlled by the dam, has a simple channel, and appeared to function as an erosional habitat. Compared to site N, lower temperatures and the comparatively low habitat heterogeneity coupled with a reduced diversity and abundance of food resources were likely imported factors restricting species diversity, as also illustrated in other investigations (Armitage 1977, Armitage and Blackburn 1990). In addition, collection of chironomid eggs from the substrates also indicated that they were more important for egg deposition at site SB than at site N. Again, this is likely due to the lack of suitable habitat at this site.

The preponderance of the chironomid, *C. bicinctus*, reflects its adaptable and opportunistic nature. *C. bicinctus* can inhabit erosional areas and attach tube retreats to substrates. Trichopterans more abundant at site SB included *Hydropsyche, Potamyia*, and *Neureclipsis*, which inhabit erosional areas and are clingers on instream supports. The rough-surfaced substrate requirement of hydropsychids for retreat and net attachment (Mackay 1992)

may, at least in part, explain why they were most abundant on wood.

Zooplankton and *Hydra* were more abundant at site SB and increased after reservoir releases. In general, zooplankton are not acknowledged in stream community studies; however, they were included in this study since they appeared to be a functional part of the substrate communities. Zooplankton released from reservoirs has been shown to contribute to *Hydra* abundance, as a food resource, immediately below dams (Armitage 1977). In addition, *Hydra* appeared to prefer cleaner attachment sites as indicated by a greater abundance on artificial wood than wood at site SB, and on site SB versus site N substrates.

Downstream site (N)

In contrast, the downstream site had a more complex channel, appeared to function as a depositional habitat, had a greater diversity and abundance of habitat types, supported macrophytes, had associated wetlands, received inputs from tributaries, and experienced greater water temperatures than site SB. Many other habitats existed that were likely more favorable to invertebrates than our substrates, i.e. macrophytes, large woody debris, and sandbars, all of which also functioned as retention devices. Substrates at this site displayed more diverse and complex communities; although invertebrate abundance was lower, species richness was about twice that of site SB. At the same time, competition with a greater diversity of taxa and greater predation may have contributed to keeping the abundance of any one taxon on a substrate less than those of site SB.

Macrophytic growth and sedimentation likely contributed to colonization at site N for many taxa. The trichopteran *Nectopsyche* was greater at site N on treatments that experienced little sedimentation. *Nectopsyche* typically inhabits vascular hydrophytes and is a climber. Macrophytes should additionally benefit *Nectopsyche* as a food resource and for case construction. The dominant chironomids at site N on days 2 and 7, *Paratanytarsus* and *Micropsectra*, are sprawlers, which inhabit the surface of floating vascular hydrophyte leaves or

fine sediments. In addition, *Micropsectra* are climbers that inhabit detrital debris or vascular hydrophytes. In a study comparing benthic macroinvertebrates from four habitat types (Wolz and Shiozawa 1995), *Paratanytarsus* was associated with a seasonally indundated wetland habitat versus river channel, ephemeral side channel and river backwater; thus the neighboring wetland in this study likely contributed to the presence and abundance of this genus. By day 30, these species were present only on wood, which accumulated the least amount of sand, and *Paratendipes* spp. dominated all other treatments. *Paratendipes* occurs in depositional areas and burrows in fine sediments. Simpson and Bode (1980) state that many species of Chironomini (including *Paratendipes* spp.) are adapted to warm standing water and can withstand periods of anaerobic conditions. Temperatures at site N increased from 15°C on day 7 to 28°C on day 30 and the water level had greatly decreased, whereas temperatures at site SB were 11.5°C on day 30. In addition, they noted that *Paratendipes albimanus* was in greater abundance in depositional areas where fine detritus accumulated.

Oligochaetes

Oligochaetes mostly feed on bacteria living in soft sediments (Wolz and Shiozawa 1995) and artificial wood in our study was typically in greater contact with sediments. At site N, artificial wood immediately supported a greater abundance of oligochaetes by day 2 than other substrates; however, abundance decreased with substrate burial. At site SB, increases occurred only for artificial wood during the first week, and by day 30 leaf packs and artificial wood, supported a greater abundance than artificial leaves, thus leaf biofilm may have become more important at that time. Abundances were also greater at site N (wood, day 2) where greater sedimentation and decomposing organic matter occured; however, day 30 abundances were greater at site SB on artificial wood, apparently due to burial at site N.

Refuge and alternate food resources at the substrate level

Abundance and species richness were positively correlated with POM accumulation.

These results support the contention of Macan (1974) that animals are more numerous in places where detritus accumulates. Overall, organic wood served as a more effective refuge for invertebrates, increasing habitat and microhabitats, providing a greater abundance and diversity of potential food resources, and leading to greater invertebrate abundance and species richness. In a study by Phillips and Kilambi (1994), greater invertebrate production resulted on snags than benthic habitats or leaf packs and chironomids and simuliids were the most common dipterans; our study also supports these results. However, zooplankton and Collembola were found in greater abundance in leaf packs. Leaf layering within a pack may offer microhabitats that sufficiently protect these smaller-bodied invertebrates from the water current, as well as support fewer predators and competitors than the other substrates. In addition, two larval fish were collected from site N leaf packs (leaf and artificial leaf) on day 30, indicating its use for refuge since nutrition was derived from egg sacs. Gawne (unpub.) also collected several small fish from leaf cages, which likely served as a substrata for refuge.

POM accumulated in far greater amounts on substrates at site N, thereby increasing invertebrate abundance and diversity, but these substrates are susceptible to burial and thus were available for relatively short periods of time. Of all treatments, organic wood at site N accumulated the greatest amount of POM by day 7. Within site N organic wood was the least susceptible to burial; thus it became the most successful substrate in terms of species richness. The percentage of POM remaining on day 30 was positively correlated with sediment accumulation; this may have prolonged the ability of substrates experiencing burial to support some taxa, as evidenced by artificial wood, which experienced the greatest burial.

Organic substrate influences on colonization

Abundances of some taxa and species richness were at times greater on organic versus inorganic substrates, including total invertebrates, chironomids, and total other insects (*sans* chironomids) on site N wood (day 7), and oligochaetes on site SB leaf packs (day 30). Greater

biofilm development was noted on organic substrates and provided an additional food source, which in turn may have increased invertebrate colonization. This is supported by Hax and Golladay (1993), who suggested that organic substrata biofilm is nutritionally superior to inorganic substrata, and found a correlation of macroinvertebrate densities with measures of biofilm development; wood had the highest densities of invertebrates and biofilm showed the strongest positive correlation, whereas a weaker association between invertebrate densities and biofilm were noted on leaves. Many of their invertebrates were of the same taxa as those reported here, namely chironomids, *Baetis*, *Caenis*, *Stenonema*, *Nectopsyche*, amphipods, and gastropods.

Indications that organic characteristics of substrates were more important at site SB than at site N for insect taxa during the first week, coincided with less instream vegetation and less drift POM at site SB, as well as lower decomposition rates. Due to a lower diversity and abundance of food resources at site SB, biofilm would be expected to increase in importance.

By day 30, leaf packs had negative effects on invertebrate colonization, and decomposition stage and thus biofilm quality of leaves may be a contributing factor. For example, chironomid abundances indicated that although leaf packs were important for colonization during the first week, wood became more important after day 30. Initially, the faster decomposition rates of leaves may have been beneficial. If "water quality conditions" defined by the biotic index are redefined as "substrate conditions", then at site N, organic substrates offered the highest quality substrates by day 2; however, leaf packs (along with artificial wood) at site N were of the poorest quality by day 30. At site SB, leaf packs from days 30 and 60 were of the poorest quality of all treatments. This may indicate that the substrate quality of leaves decrease as they further decompose; however, sediment accumulation at site N contributed greatly to the poor quality.

2.3.4. *Invertebrate Diets*

2.3.4.1. Food Resources

Leaves and wood

The results of this field study agree with the previous microcosm experiment discussed in chapter 1 and with the prairie model describing invertebrate/microbial relationships with leaf packs (Ch.1, Fig. 1b.). Hill et al. (1988, 1992), and Short et al. (1984) concluded that microorganisms contributed to leaf breakdown to a greater extent than macroinvertebrates in prairie streams. Similarly, this study indicates that direct feeding of cottonwood by macroinvertebrates was insignificant: 1) L and W were intact at the end of the study, 2) leaf/wood particulates were infrequently encountered in invertebrate guts and were low in abundance; less than 10% of larvae from organic substrates contained leaf/wood particulates, 3) leaf/wood particulates in the guts were typically less than 1 mm and thus may have been derived from drift FPOM rather than from the experimental substrates; this is further supported by the fact that primary consumers of this material were hydropsychid and polycentropodid trichopterans that are sedentary with fixed retreats and capture nets, strain food particles from the current, and show little food selectivity (Wiggins 1996), and 4) Shredders of detritus (SHD) overall represented less than 1% of total invertebrates at site N, and 0% at site SB; this included early instar Tipulidae which contained no cw material and were collected from inorganic substrates

Significant substrate and time effects occurred from site SB only; leaf/wood particulates in trichopterans from artificial wood (day 7) were more common than from: 1) wood, which suggests its origin was from drift, and 2) artificial leaf packs, which coincided with POM accumulation on substrates. Data from artificial wood chironomids suggested that leaf/wood particulates were more abundant in drift at site N versus site SB by day 2. Insignificant substrate and time effects for leaf/wood particulates at site N, suggests that consumed leaf/wood material

were primarily from sources other than the leaf pack and wood treatments.

At site SB, a significantly larger percent of trichopterans from leaf packs (day 7), and chironomids from wood (day 30) contained leaf/wood particulates than their inorganic counterparts, which suggested that organic substrates at site SB directly contributed this material to a small percentage of larvae. This coincided with lower POM accumulation and may also be affected by stage of decomposition. A subsequent decrease in the percentage of SB wood chironomids with leaf/wood indicated that the contribution became insignificant by day 60.

Wood breaks down very slowly and may not have been at a stage that is preferred by wood consumers. Dipterans (i.e. chironomids) are the dominant consumers of submerged or semi-submerged wood. Phillips & Kilambi (1994) showed that the taxonomic composition of dipterans inhabiting wood changed as it passed through five stages of decay. Application of their method for characterizing decay stage indicated that wood in this study was still in the earliest stage of decay.

Particulate organic matter (POM)

Troelstrup (1985) examined food habits of both zooplankton and macroinvertebrates on the same stretch of the Missouri River. In his study, POM was the predominant gut content in all invertebrates, with the exception of *Dineutus* sp. adults (predaceous beetles). This study supports his conclusion, and we additionally separated the POM into subcategories: CPOM, FPOM, and biofilm. Biofilm and FPOM were the most frequently encountered and abundant gut contents. CPOM (primarily from macrophytes) was relatively common in some taxa from site N.

Biofilm was a main gut content in most taxa, and organic wood substrates contributed a greater quantity and likely quality of biofilm than the other substrates. Biofilm from invertebrate guts from organic versus inorganic, and wood versus leaf pack substrates were typically darker in color and in larger quantity. For example, trichopteran guts (day 2-30) indicated that 43% of larvae from leaf packs and 66% larvae from wood contained biofilm. Fungi were noted in greater

quantity in the darker biofilms from invertebrates of organic substrates, especially wood. The darker staining of organic substrate biofilms, suggests that leaves and wood likely contributed to biofilm development through leachates (DOM) and FPOM. This food source should be immediately utilized by invertebrates if DOM provides nutrients even before bacterial colonization (Mackay 1992). Our results are supported by Sinsabaugh (1991) who states that organic substrata biofilm may differ substantially from that on inorganic substrata due to heterotrophic energy flow (resulting in greater microbial and fungal biomass), fungi are a significant food resource for stream invertebrates, and wood has a greater potential for biofilm development than do leaves. Tank et al. (1993) also observed higher microbial respiration on decomposing sticks than leaves.

FPOM was also a main gut content. Many authors have discussed the importance of FPOM as an invertebrate food source in stream systems. Vannote et al. (1980) states that FPOM is the primary energy resource in large rivers. In addition, the large majority of invertebrate taxa in this study are considered FPOM collectors. Patterns were similar to the biofilm results. FPOM was typically darker and in larger quantity from invertebrate guts from organic substrates, especially from wood, indicating contributions from these substrates. FPOM appeared to be consumed in larger quantity when it was darker in color, and there was evidence to suggest that the presence of this darker FPOM supports a greater abundance of chironomids. It is likely then, that the more darkly stained FPOM originating from organic substrates was a higher quality food resource.

Other vegetation and fiber were relatively common in site N trichopterans, and were most frequently encountered from substrates in debris dams (wood). Decaying vegetation from local macrophytic growth appeared to be a relatively important food source for the invertebrates, as suggested by gut contents. Macrophytes can be an important source of detritus in large rivers and floodplains, and the decomposition and fate is similar to that of terrestrial leaves (Allan 1995,

Polunin 1984). Andersen and Sedell (1979) found that macrophytes can account for 9-13% of stream productivity and for almost 100% of primary production in polluted unshaded sections of some rivers. In addition, decomposition rates are typically twice as fast for macrophytes as terrestrial leaves. Detritus in general has been shown to be a main food resource in some of the same taxa identified in this study: *Hydropsyche*, *Potamyia*, *Stenonema*, *Baetis*, and *Tricorythodes* (Shapas and Hilsenhoff 1976). Historically, primary production driving Missouri River communities was likely a function of terrestrial macrophytes and emergent aquatic plant production (Hesse et al. 1989).

Terrestrial grasses may also serve as a food resource. "Other vegetation" within site SB trichopterans appeared to be primarily grass. Although this material was rarely encountered the first month, the percentage of trichopterans with other vegetation greatly increased from artificial leaf packs and especially from wood and artificial wood by day 60. The fact that this material was in low quantity in guts may have more to do with low availability. Gawne (unpub.) concluded that grass decomposes more rapidly in this system than cottonwood leaves, and Hesse and Schmulbach (1991) point out that historically, before decoupling of the Missouri and its floodplains, prairie grasses were introduced to the river during flooding events.

Diatoms

Initially (day 2, day 7), diatoms were commonly encountered in larvae from site SB (primarily chironomids and hydropsychids). Troelstrup (1985) noted that diatom occurrence was relatively common in hydropsychid caddisflies and heptageniid and baetid mayflies; however ephemeropterans in this study did not contain diatoms. Observations by Gawne (unpub.) indicated that diatoms were a main component of drifting POM at site SB. Diatom consumption pattern follows that of biofilm, thus diatoms were likely a component of the biofilm. As with biofilm and FPOM, evidence suggests that a greater abundance of diatoms may support a greater abundance of chironomids at site SB. As in Troelstrup (1985), diatoms in zooplankton were

rarely encountered; zooplankton in our study indicated that less than 5% contained diatoms.

Animal material

Animal material (primarily early instar chironomids and copepods) was also an important food resource at site N. Zooplankton released from the reservoir acted as an additional food resource for some taxa, i.e. *Hydra* and some species of Chironomidae and Trichoptera. Troelstrup (1985) found animal material to be a relatively important food resource for Coenagrionidae nymphs and Polycentropodidae. He stated that POM and diatoms, also found in substantial quantity in the guts of these taxa, may be due to a combination of coincidental ingestion and acquisition from prey items.

Biofilm effects on macroinvertebrate feeding habits

Biofilm development on the substrates may be a primary factor preventing substrate surfaces from skeletoniztion by invertebrate feeding and physical abrasion. In a preliminary experiment using distilled water, cottonwood leaves did not contain an obvious biofilm and were skeletonized by *Hyallela azteca* and physid snails. The leaf material was clearly visible in the guts of these taxa. If reproduction rates are used as an estimate of food quality, then this material was of poor quality since abundance of these taxa were approximately the same after one month. In contrast, the microcosm and field studies suggest that sufficient conditions exist in the Missouri River to develop a biofilm that provides alternate food resources and prevents skeletonization of the leaves. As described in chapter 1, snails in microcosms were found on and appeared to consume biofilm that coated plastic lining the streams. Their presence away from the leaves and gut analysis of FPOM and biofilm not stained by leaf leachates may indicate that these snails are not likely to consume leaf material if alternate resources are available. The field study supports this contention for a variety of taxa. In addition, as stated in chapter 1, macroinvertebrate success in terms of survivability, growth, and reproduction was fairly high in

the microcosms, likely due to a nutrient rich biofilm and FPOM as food resources. Additionally, all evidence suggests that water at site SB is lower in nutrients than that of site N, and biofilm ingestion by larva from site N was greater. Although percentage of chironomids with leaf material were low, a larger percentage from SB leaf packs on days 7 and 30 contained leaf particles in their guts than from site N. This may further indicate that leaf particulates may be consumed when other resources (i.e. biofilm and accumulated POM from the drift) are low.

Changes in biofilm quality and quantity

Percentage of chironomids with biofilm were affected by time at site SB only, and was likely due to slower biofilm development characteristic of this site. Results imply that biofilm became a more important food resource to SB chironomids over 30 d, more quickly from the wood treatments, likely due to increased quality and quantity of this material. Trichopterans with biofilm decreased in proportion from SB leaf packs (day 30 to 60), and from N leaf packs (day 2 to 7); however, those from wood were not affected by time. This may have been due to the relatively rapid decomposition of leaf packs, especially at site N.

Opportunitstic feeding

Gut contents reflected characteristics of site location. In general, a greater percent of SB larvae contained diatoms than those of site N. At site SB, diatoms and FPOM appeared to be the primary food resources over the first week, followed by a shift to FPOM and biofilm thereafter. Diatoms are introduced at this site through reservoir releases. In contrast, a greater percent of site N larvae contained fiber, other vegetation and biofilm. Site N contains both autochthonous material and inputs of a variety of material from other sources. In addition, conditions were more favorable for biofilm development at site N. Faster breakdown rates and more abundant and diverse sources of biofilm products (i.e. macrophytes and other terrestrial material) contributed to a significantly larger percent of Chiron with biofilm by day 2 for all treatments.

If the invertebrates were feeding as true opportunists, then gut content analyses indicates varying success among the substrates for providing specific resources. Frequency encountered, quantity, and quality (i.e. biofilm characteristics) of gut contents were considered. Comparisons of invertebrates from wood and leaf packs indicate that wood is a more successful biofilm and diatom substrate, and additionally offers a greater abundance and diversity of detritus (i.e. "other vegetation") from drift. Of course there is always an exception, and evidence towards resource selection versus opportunistic feeding included consumption of animal material by predators and selection of diatoms by some chironomids.

Time effects for fiber may, in part, be indicative of changes over time in the periphyton community (recall that some fibers were later identified as filamentous algae). At site N, day 7 trichopterans from inorganic substrates consumed less fiber with increased POM accumulation. Although relatively scarce, filamentous algae were more common at site N and these results may indicate less association with the periphyton with increased accumulated POM. Troelstrup (1985) also noted the rare occurrence of other algae (excludes diatoms) in invertebrate guts; occurrence was always less than 1%. In contrast, other fiber was likely detritus that accumulated from drift; a larger percent of SB trichopterans from leaf packs and SB chironomids ingested fiber when accumulated POM had increased on substrates.

Disturbance effects on food resources

When reservoir releases increased by day 30, subjecting site SB substrates to high shear forces and fluctuating water levels, and site N substrates to burial, gut content differences between larvae of site SB versus site N became insignificant. Diatoms, like the accumulated POM, were likely scoured from SB substrates; this was evidenced by a significant decrease in percent invertebrates with diatoms. By day 60, further decreases in percent trichoptera with vegetation and biofilm (from artificial wood and leaf packs, respectively) coincided with an increased current velocity and depth, which adversely affected POM accumulation and possibly

biofilm quantity. Sedimentation at site N affected biofilm consumption; artificial leaf packs were less susceptible to burial than leaf packs and artificial wood, and overall occurrence of biofilm from artificial leaf chironomids approached that of wood. Overall occurrence of biofilm in trichopterans was actually higher from artificial leaves than from other substrates.

Water velocity and sedimentation can further explain why skeletonization of leaves did not occur by scrapers such as amphipods. In streams, taxa such as *Hyallela* occur in areas with reduced current (Andersen and Sedell 1979). At the time of substrate removal on day 30 at site N, water velocity and depth had decreased and the formation of semi-pools around some substrates resulted in further decreases in flow. *Hyallela* occurred in relatively large numbers on two of three wood replicates, whereas burial effects on leaf packs prevented amphipod colonization. Infrequent periods of low flow at the substrate level and increased burial should decrease lengths of time that *Hyallela* can effectively utilize the substrates and therefore decrease contributions to organic matter processing.

The ability of wood to provide a more stable habitat for invertebrates in a system driven by disturbance is emphasized by a significant increase in percentage of chironomids with animal material (SB wood, day 30 to 60). This implies that wood was able to support more mature larvae since diet may shift to greater animal consumption in later instars.

2.3.4.2. Trophic Relationships

Most aquatic insects are opportunistic feeders rather than belonging to a single functional feeding group (FFG). Feeding habits for many species shift with maturation, for example the majority of benthic species ingest detritus while young, but shift to algal or animal material as they mature (Andersen and Sedell 1979). Thus type of food resource available and life stage of the invertebrates can greatly impact the interpretation of study results.

In general, gut analysis appeared to coincide with the FFGs previously described (Merritt and Cummins, 1996); however, *Cricotopus* spp. guts at site SB indicated that SHH feeding was

likely insignificant. In addition, taxa that are considered SHD, or possible SHD, did not appear to be functioning as such, rather as collectors and/or as scrapers. Zooplankton that had the potential to feed as predators also did not appear to be doing so to a significant extent. Many groups with multiple feeding modes were early instar larvae and appeared to be feeding primarily as collectors, thus the percent of invertebrates representing other FFGs may be overestimated.

The majority of the invertebrates collected from sites SB and N substrates were collector-gatherers (CG), up to 55% and 57%, respectively. Hax and Golladay (1993) recorded a mean of 55% CG from wood and leaves at a slow current site of a 4th order New York stream; however, zooplankton was not considered a part of their community, and if zooplankton are excluded from these data (as in many investigations), then CG represents up to 89% and 73% of the invertebrates, respectively. Growns and Davis (1994) found CGs to be 56% of the total fauna collected from a Western Australian stream, and two of their taxa could be considered zooplankton. Zooplankton were included in this study because they appeared to be utilizing the substrates and they serve as a food source for macroinvertebrates and fish. Troelstrup (1985) stated that although several taxa in his Missouri River study belonged to multiple functional feeding groups, the predominant group was CG. Hesse et al. (1988) stated that CG, CF, scrapers and shredders are the major FFGs of Missouri River macroinvertebrates. This study indicates that scrapers were relatively common at site N, but rare at site SB. SHH had the potential to be high at site SB due to the preponderance of *C. bicinctus* (late instars may function as SHH); however, a more diverse assemblage of invertebrates at site N had the potential to function as SHH.

Organic substrate and accumulated POM contributions to FFG dynamics

Utilization of leachates, possibly in flocculated form, is suggested within the site SB zooplankton community and site N macroinvertebrate community on day 2 when CF taxa were in greater proportion on organic substrates. An increase in scraper abundance by day 7 may

coincide with biofilm development, especially on wood at site N. Increases in CG, SHH, and Pred coincide with increasing POM. In this study, an overall greater abundance of CGs on wood coincided with greater FPOM accumulations, which agrees with Mackay (1992); CGs colonize substrates as fine detritus accumulates.

Disturbance effects on the FFG community

Increased reservoir releases at site SB by day 30 resulted in decreased abundances in all macroinvertebrate FFGs and an increase in zooplankton (CF and predators). Increased water depth and velocity by day 60 coincided with a further decrease in macroinvertebrate CG and SHH groups, whereas the CF/pred groups increased on all but L; however, relative abundances indicate that the macroinvertebrate FFG pattern remained similar throughout time.

Increased sedimentation at site N reduced abundances of the various FFGs; the exception was to wood, which experienced the least amount of burial, and CF and CG increased. In terms of relative abundance, FFG patterns were dependent on extent of substrate burial; as burial increased, proportion of CF and scrapers decreased, and CG and predators increased.

An interesting observation, likely linked to the varying affects of disturbance between the two sites, was the CG, CF, and predator dynamics of Chironomidae and Trichoptera. Percentages of CG chironomids and CF/predator trichopterans were greater on site SB substrates, whereas CG trichopterans and CF/predator chironomids were greater at site N. Thus, although particular taxa contributions to specific FFGs varied between sites, the FFG dynamics remained similar. In addition, a much larger diversity of taxa existed within the various FFGs at site N.

Flow refuge

A greater diversity and abundance of habitats at site N versus site SB, greater POM accumulations on site N substrates, and greater accumulations on wood substrates versus those of leaves offered increased refuge from water flow. The scraper results offer an excellent example;

scrapers were more abundant at site N, and on day 7 (when POM accumulations were at their highest) percentage of scrapers reached its maximum, was greatest on wood, and became even larger in proportion than CFs. This is supported by the results of Growns and Davis (1994) who discovered that they were able to assign most taxa with the same FFG to the same flow exposure group. Scrapers were described as flow faculatives, "spend most of time on substrate surface usually with adaptations to lessen drag but able to move into low flow areas". Thus the stability of wood, should offer additional benefits to these organisms, i.e.
like the framework of a houseboat.

CGs and shredders are flow avoiders (live within the substrate; Growns and Davis 1994) and so should be affected similarly. Although relative abundances (day 2-30) of the various macroinvertebrate FFGs were similar among substrate types at site SB, when zooplankton were included CG and SHH were at least twice as high on wood and CF were nearly twice as high on leaves. The more stable wood with areas of low flow within accumulated POM allow CG and SHH to move into areas of reduced velocity. In contrast, greater CF zooplankton on L coincides with their ability to utilize the relatively smoother surface (Mackay 1992).

2.3.4.3. Conclusions

Cottonwood material did not serve as a direct food source for Missouri River macroinvertebrates, but rather indirectly supplied nutrients through biofilm development and DOM flocculation. In fact, leachates from cottonwood appeared to have served as an immediate food source to some CF macroinvertebrates and zooplankton. Although various measures differed substantially between sites SB and N, relative abundances of FFGs were quite similar. Collectors were highly dominant, and the higher percentage of SHH at site SB indicated potential only, since gut analyses indicated that *Cricotopus* spp. were not feeding as such. The only substantial difference was the higher abundance and proportion of scrapers at site N, primarily due to ephemeropterans. Although scrapers can function as SHD, gut analyses and substrate condition

indicate that even for this FFG, ingestion of cottonwood was insignificant. Scraper feeding on biofilm may have enhanced decomposition rates at site N versus site SB, but overall results support the contention by Hill et al. (1992) and Short et al. (1984) from north central Texas, that microbial activity is the most important biotic agent of litter decay in prairie streams.

Substrates served as habitat resources for invertebrates, providing alternate food sources and refuge. Biofilm development on cottonwood appeared to contribute significantly as a food resource, as did material that accumulated on the substrates. Wood acts as a better retention device, supporting a greater abundance and diversity of food resources, habitats, and microhabitats. W also provides a more favorable substrate for biofilm development. Macrophytes were also consumed and may be an important food resource. Diatoms were initially an important food resource upstream at site SB and zooplankton originating from the reservoir served as a food resource for predators.

In general, it appears that disturbance imposed by impoundment necessitates opportunistic feeding. In addition to the barrier effect of dams, shear forces of reservoir releases and highly fluctuating water levels negatively impacted food availability for invertebrates. FPOM and biofilm were the dominant gut contents and accumulated detritus was consumed when available.

2.3.5. *Comparison With Existing Models of Lowland Rivers*

Comparisons with river models will focus on spring-summer dynamics in this river reach, since data from this field study were collected from early May through early July, in the middle Missouri River.

Historic Middle Missouri--During the pre-control era of the Missouri, allochthonous organic material would have been abundant in the river channel during the spring and summer, due to flooding events occurring in March and June (Schmulbach et al. 1992). At that time, 75% of the middle Missouri floodplain was forested, dominated by cottonwood, with the remaining

consisting of wetlands, grasslands, and shrublands (Johnson 1998). Flooding events brought in trees, grass, marsh plants, and rich organic soils, and large amounts of dissolved and suspended organic matter from soils carried by tributaries to the main channel (Hesse and Schmulbach 1991). Production within the floodplain was responsible for the majority of riverine animal biomass (Junk et al. 1989, Hesse & Sheets 1993). Thus, it seems likely that the Flood Pulse Concept (FPC; Junk et al. 1989), for large river structure and function, would have applied to the Missouri.

Present Middle Missouri--Dams have altered the natural hydrologic cycle; minimum flows occur in the spring and high releases occur in the summer (Johnson 1998). From March to August, power peaking discharges and lengthy dewaterings subject the reach between Fort Randall and Gavins Point Dams to highly fluctuating water levels (Hesse et al. 1988). These events were observed at field sites, and when experimental units were left exposed. Floodplain forests have been cleared for agriculture and most of the wetlands have been lost (Schmulbach 1992, Johnson 1998). Water leaving reservoirs to the unchannelized reach is nearly devoid of nitrate and phosphate (Schmulbach 1992); thus the source of major nutrient inputs predicted by the River Continuum Concept (RCC; Vannote et al. 1980) and the FPC do not apply here. The Serial Discontinuity Concept (SDC; Ward & Stanford 1983) and Vannote et al. (1980) state that dams should shift predictions of the RCC up or down the stream-order axis. Furthermore, the SDC states that on large rivers, dams reduce downstream turbidity, thereby increasing aquatic plant abundance and causing a shift in the system toward the character of a mid-sized river (Johnson et al. 1995). The Riverine Productivity Model (RPM; Thorp & Delong 1994) states that organic carbon from a combination of both local primary production and direct inputs from the riparian zone (including DOC) significantly contribute to secondary production in large rivers. The RPM also suggests that invertebrate composition and abundance differ among sites due to habitat characteristics and types of organic matter present; thus dependence on autochthonous or

allochthonous material should vary among sites.

New Model: Middle Missouri River Concept (Fig.23)--Existing river models are primarily theoretical and lack extensive corroborative data. Wetland, backwater, and tributary contributions in these systems appear to be neglected. The river reach investigated in this study was unchannelized and lay between two dams. Sunshine Bottom (SB; upstream field site) was located above the influence of tributaries, and a simple channel with no macrophytic growth characterized the river. This reach was dependent upon water releases from Francis Case Lake, which was relatively cold, clear and low in nutrients. In addition, zooplankton and phytoplankton were introduced from this reservoir. Cladoceran and copepod densities in this reach result from upstream reservoir releases and decrease downstream due to reduced survivability and availability of zooplankton (Schmulbach et al. 1992). Invertebrate assemblages were similar to those predicted for large rivers by the RCC, greatly dominated by collectors and displaying a semi-lentic nature. Species richness was low and invertebrates were dominated by chironomids, oligochaetes, zooplankton, and collector-filtering trichopterans. Suitable invertebrate habitat was lacking. In contrast to the RCC, the results of this study suggest that along with FPOM, diatoms appeared to be a main food resource, at least in May, and biofilm became increasingly important up to 30 d. In addition, FPOM was not likely to have come from upstream processing of CPOM, rather from more local sources of DOM flocculation. By early July, degradation of the riverbed at SB caused by sediment-free releases from the reservoirs was obvious, the channel had moved and water depth and velocity had greatly increased.

Niobrara (N; downstream site) was located below the confluence of tributaries, and current velocity and temperature had increased. Unlike the upstream site, a complex channel with sandbars, islands, macrophytes, and associated wetlands and backwaters characterized the site. Again, collectors (as for SB) dominated, but scraping invertebrates (Ephemeroptera) had increased. This invertebrate community appeared to be similar to that predicted by the RCC for

medium-sized rivers, the SDC, and the RPM. It is possible that functional feeding group proportions at this site may have even more closely resembled those predictions (i.e. a greater percentage of scrapers), had community assessments been based on extensive sampling (i.e. cross-channel density). In fact, scraping invertebrates from wood and artificial wood in this study represented 29% and 30%, respectively, in May before reservoir releases increased.

In addition, a greater assemblage of taxa that may function as shredder-herbivores were present, and species richness of invertebrates was approximately twice that of site SB. Riverine habitat was more abundant and diverse. Detritus from local macrophytic growth supplied a relatively important food source to the invertebrates, as indicated by gut analysis. Inputs from tributaries may have also contributed to invertebrate food resources. Material that accumulated on substrates was greatest in May and consisted of macrophytes, allochthonous vegetation and some algae. In addition to a greater abundance and diversity of POM as a food source for site N invertebrates, greater nutrient concentrations in the water and warmer temperatures at site N favored microbial growth and activity, which in turn aided in organic matter breakdown. An important result of this process was the formation of nutrient rich biofilms on substrate surfaces that served as an invertebrate food resource. Breakdown rates of cottonwood were greater at this site, and biofilm and associated fungi were more abundant in larval guts. As with the upstream site, direct feeding of cottonwood was insignificant. Unlike the upstream site, diatoms were rarely ingested. The collection of larval fish, at site N, indicated that experimental substrates served as a refuge for fish, which were likely more abundant at site N. Sediment deposition occurred at site N, as evidenced by decreased water depth and burial of substrates. By June, substrates were partially buried, and by early July all of the substrates were deeply buried in the riverbed. Sumsion (1990) states that in general, dams decrease depth and growth of vegetation downstream.

The RCC, SDC, and RPM all contribute to a better understanding of Missouri River

structure and function. These results suggest that this river reach functions similarly to the RCC model in reverse. The upstream site functions as a large river and the downstream reach functions as a medium-sized river; however, due to impoundment, it is unlikely that inefficiencies of upstream CPOM processing are a significant food resource, as described by the RCC. Rather autochthonous production and inputs from local sources are the major energy sources. It appears that the combination of tributaries, wetlands, and backwaters may function as the RCC's headwater stream, and along with local macrophytic growth, causes the large river to function as a medium-sized river. A more complex channel at this site should also contribute to the shift in community structure. It is possible that autochthonous rather than terrestrial material may be supplying the greatest proportion of food for invertebrates from May through early July; however; further investigations need to be conducted to determine precise sources.

2.3.6. *Management Implications Regarding Detrital Additions*

Although diatoms at site SB appeared to be an important food resource on days 2 and 7, and macrophytes appeared important throughout the study at site N, it is "unlikely that sufficient autotrophy exists to replace the lost floodplain production" (Hesse and Sheets 1993). Cottonwood additions offer food resources via breakdown by leachates and microbial activity, and support temporary habitats. *Populus* and *Salix* woodlands are failing to regenerate on the Missouri and its tributaries since recruitment of these trees was dependent on channel meandering and point-bar formation associated with spring flooding events (Johnson 1998). Thus, as suggested by Hesse and Sheets (1993), the loss of organic matter and nutrient supplies to the Missouri may be temporarily replaced by the introduction of leaves and trees in the form of detritus to the river. Our study indicates that large woody detritus would be of greatest importance, and agrees with a Georgia river study that emphasized the importance of wood as a habitat resource; although submerged wood made up only 4% of the total habitat, it supported 60% of the invertebrate biomass (Benke et al. 1985). Leaf accumulations were an important

habitat resource for the smaller-bodied invertebrates, including zooplankton. Since zooplankton serve as a food resource for predacious invertebrates and fish, contributions of leaves should not be overlooked. Additions of cottonwood with attached branches and leaves should maximize contributions to the river fauna. In addition to its function as a direct habitat resource, large woody debris controls routing of sediment and channel hydraulics, which contribute to stream heterogeneity and habitat complexity (Hedman and Van Lear 1990). Furthermore, detrital accumulations in woody debris dams are not only important for invertebrates, but offer important habitat features for stream microflora and fish (Gurtz et al. 1988).

Results of this study indicate that invertebrates important in the diets of many fish, i.e. chironomids, oligochaetes, and crustaceans, benefit from the addition of stable substrata. Another benefactor that may be of concern is Simuliidae. Simuliids increased with disturbance due to reservoir releases. In June and July, simuliids occurred in large aggregations on a few wood substrates. In addition, large aggregations occurred on the conduit poles at site N during the same time. Phillips & Kilambi (1994) also list two studies that reported Simuliidae to be relatively common on snags. As mentioned in Ch. 1, potential increases in Simuliidae, with increased organic matter addition, may be of concern due to their reputation as a pest species and their ability to vector disease. This would be especially true if predators such as *Cardiocladius* were rare, as indicated by our results. *Cardiocladius* is a relatively sensitive chironomid species (tolerance value = 4) and may not increase in abundance if conditions within the Missouri River are not improved.

Disturbance caused by water releases from the reservoir was the primary driving force shaping invertebrate composition on substrates. The efficacy of detrital additions to the Missouri River is questionable. Upstream at site SB, the riverbed is highly unstable. DOM would be rapidly introduced through leachates, but further breakdown is comparatively slow and introduced material is likely to be rapidly flushed downstream. Material not flushed immediately

downstream and/or buried, is likely to be exposed for periods of time due to highly fluctuating water levels. Downstream at site N, cottonwood breakdown occurs much more rapidly, but the potential for burial increases. These effects contributed to a reduction in invertebrate abundance, species richness, and environmentally sensitive species.

For introduced material to be efficiently used, restoration efforts of important ecological features of the Missouri (i.e. hydrology and habitat), need to be implemented or strengthened. In addition, habitats associated with rivers such as backwaters, wetlands and side channels can contribute substantial biomass to river systems (i.e Wolz and Shiozawa 1995) and would reduce the need for artificial inputs of organic matter. In general, debris dams serve as a more important retention device in forested low-order streams, whereas riverine geomorphological features such as bars, alcoves and eddies are more important in higher order streams for retaining organic matter (Allan, 1995). It is likely that without the aid of our conduit poles to hold the substrates in place, transport and burial of the substrates would have been much more prevalent. Nutrient additions alone may not increase the biomass of the fish if litter retention and other needs of the river inhabitants are not met. In addition, further information is needed regarding quantities and sizes of woody debris that would optimize stream productivity, and its effects on channel morphology. Timing of inputs should be critical. Additional studies on the effects of different stages of wood decay on invertebrate communities would also be of value, as would investigations of seasonal and annual variations in community structure and function.

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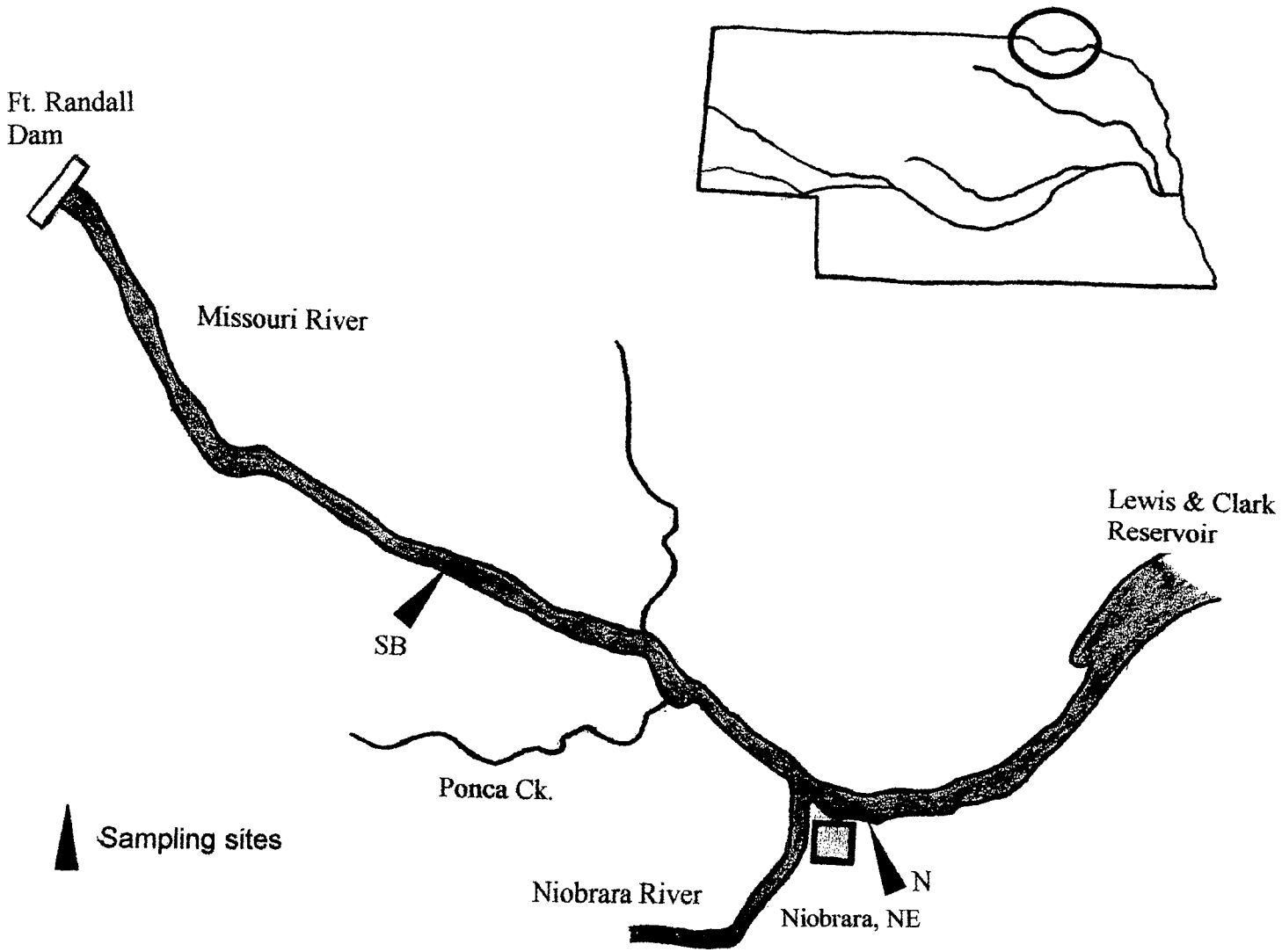


Figure 1. Map of field sites: Site SB (Sunshine Bottom; upstream) and Site N (Niobrara; downstream).

Table 1. Leaf (L) and wood (W) breakdown as described by mean percent mass loss (± SD) with time in days (d); replicates (r) = 3, except on day 60.

		Mass Loss (%)			
trt	site	d2	d7	d30	d60
L	SB	12 (1)	13 (3)	16 (2)	43 (r=1)
L	N	15 (3)	20 (4)	42 (7)	*NR
W	SB	12 (1)	12 (<1)	13 (1)	21 (1), (r=2)
W	N	13 (1)	13 (<1)	17 (1)	*NR

*NR = not recovered

Table 2. Decomposition rates of L and W based on an exponential decay model. Processing coefficients (k–values) are shown for time intervals between sampling periods. K-values are categorized as fast (f), medium (m), or slow (s) (Webster and Benfield, 1986).

		Processing Coefficients, k (d^{-1})				Overall k-values	
trt	site	d0-2	d2-7	d7-30	d30-60	d0-30	d0-60
L	SB	0.061 f*	0.003 s	0.002 s	0.010 m[r]	0.006 m	0.009 m
L	N	0.080 f*	0.012 f	0.014 f*	NR	0.018 f	NA
W	SB	0.062 f*	6.46E-5 s	0.002 s	0.003 s*	0.004 s	0.004 s
W	N	0.072 f*	0.0002 s	0.002 s*	NR	0.006 m	NA

* significant mass loss (p = 0.00-0.01)

[r] only one replicate was available for L at SB day 60

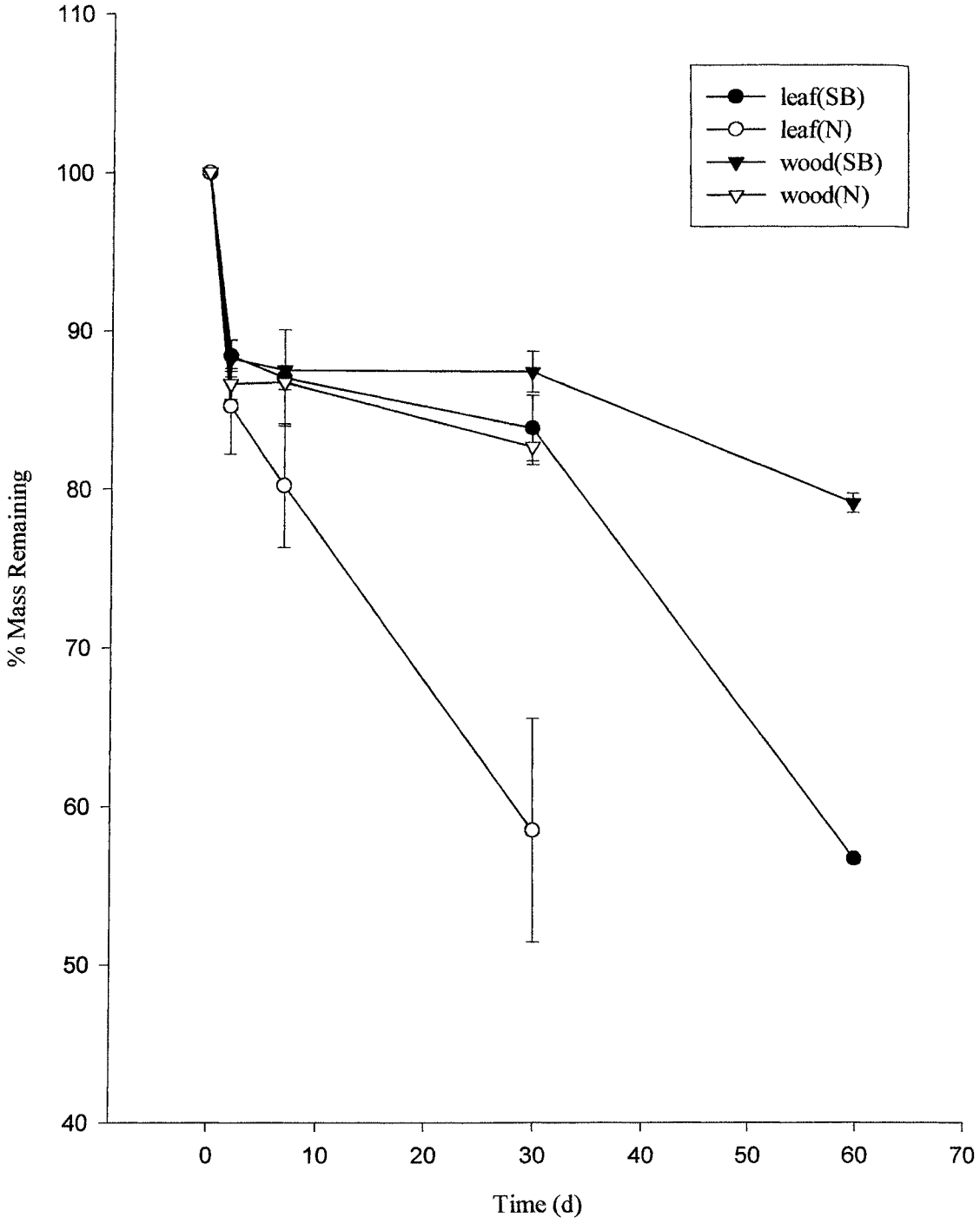


Figure 2. Leaf and wood decomposition at sites SB and N, as percent mass remaining on days 2, 7 and 30 for both sites and day 60 for site SB.

Table 3. Mean (±SD) dry mass of accumulated (accum.) organic matter in g d^{-1} and site (n=3). On day 30 many of the substrates at site N were partially buried. Dry mass (g) of sand collected with these buried substrates is included. L (leaf pack), AL (artificial leaf pack), W (wood), and AW (artificial wood).

		Site SB - Dry Mass (g)				Site N - Dry Mass (g)			
trt	**accum. material**	**d2**	**d7**	**d30**	**total d2-30**	**d2**	**d7**	**d30**	**total d2-30**
L	CPOM	0.20	0.11	0.10	0.14 (0.05)	0.91	2.37	0.68	1.32 (0.92)
	FPOM	0.03	0.02	0.07	0.04 (0.02)	0.08	0.19	0.26	0.18 (0.09)
	Sand							66.99	
AL	CPOM	0.07	0.49	0.06	0.20 (0.24)	0.55	5.58	0.99	2.37 (2.79)
	FPOM	0.02	0.06	0.02	0.04 (0.02)	0.06	0.28	0.13	0.16 (0.11)
	Sand							45.50	
W	CPOM	0.42	3.64	0.21	1.43 (1.92)	1.15	13.92	1.53	5.53 (7.26)
	FPOM	0.07	0.12	0.19	0.13 (0.06)	0.11	0.46	0.23	0.27 (0.18)
	Sand							1.01	
AW	CPOM	0.17	3.17	0.33	1.22 (1.69)	2.58	*4.76	3.72	*3.68 (1.09)
	FPOM	0.03	0.09	0.16	0.09 (0.06)	0.10	*0.51	0.51	*0.37 (0.24)
	Sand							122.53	

* One AW replicate from day 7 was not preserved; thus, the mean of two replicates was used as the third for statistical analysis

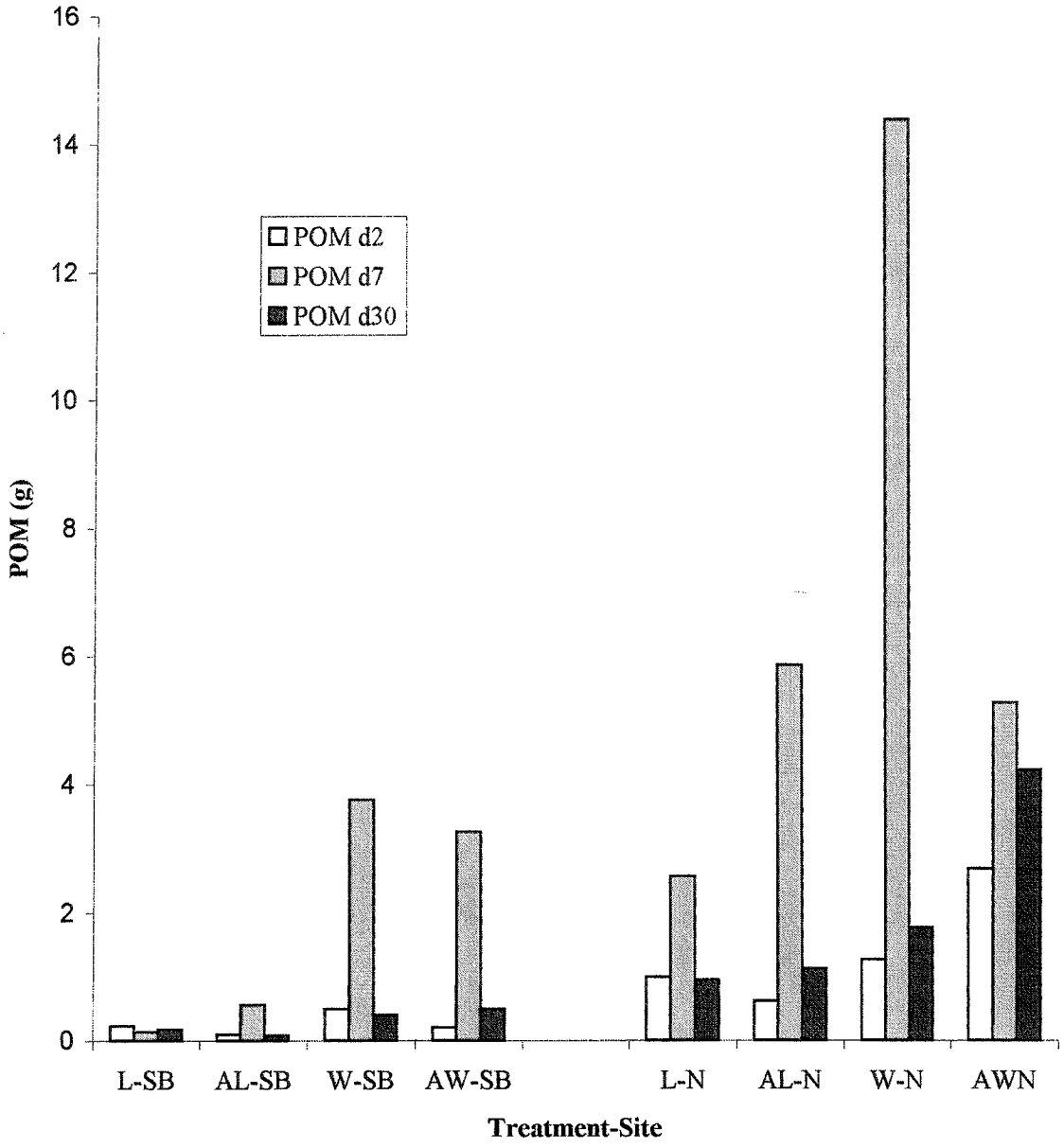


Figure 3. Mean dry mass of particulate organic matter (POM) on substrates at sites sites SB (upstream) and N (downstream) on days 2, 7, and 30. L (leaf pack), AL (artificial leaf pack), W (wood), AW (artificial wood).

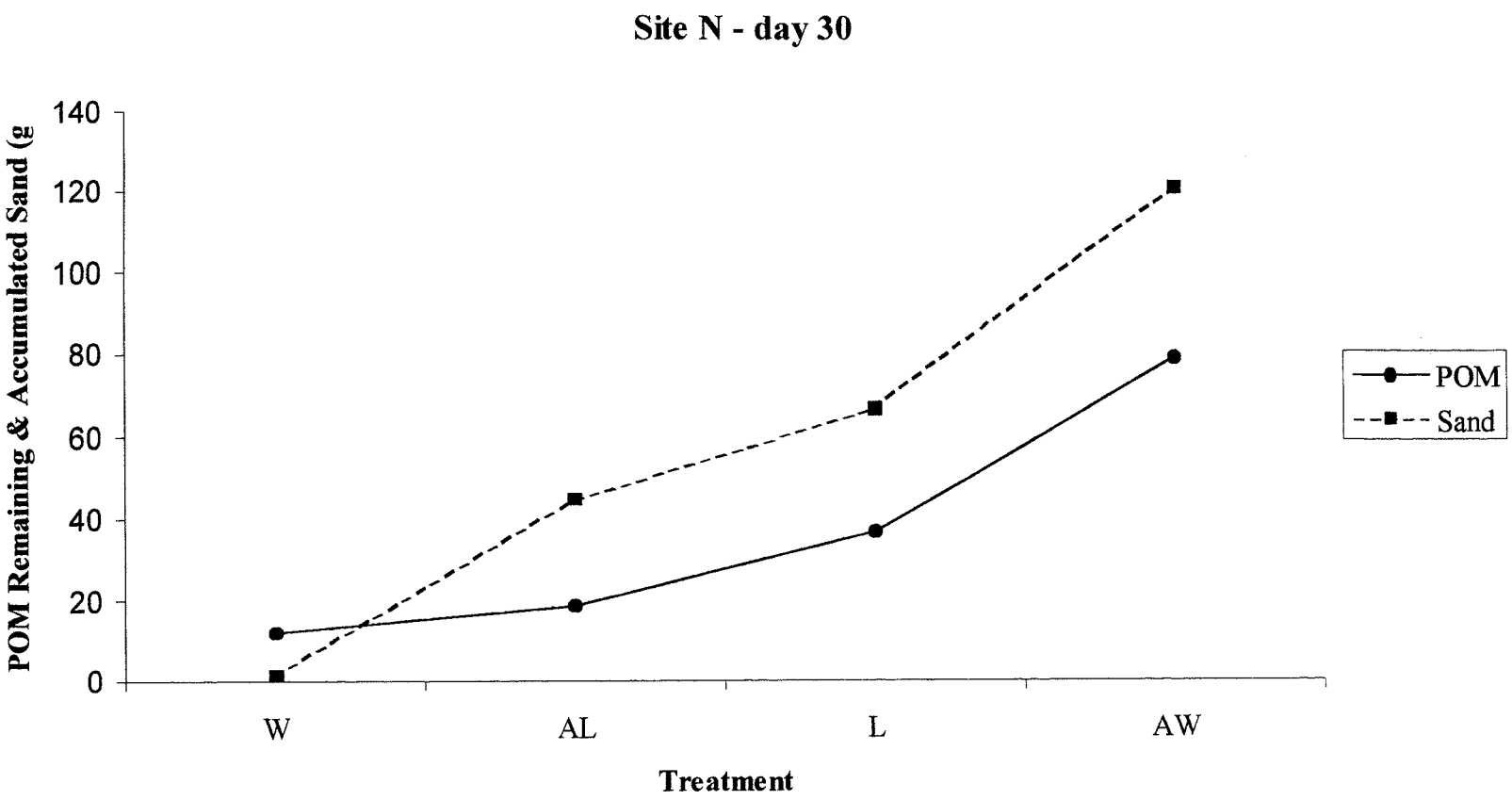


Figure 4. Percent of POM remaining on site N substrates by day 30 (based on % of day 7 POM) relative to substrate burial (accumulated sand).

Table 4. Invertebrate abundance, relative abundance (%), and functional feeding group (FFG) of the most abundant taxa from substrates at sites SB (upstream) and N (downstream).

Site SB days 2-30 (n = 36)			SB day 60 (n=7)	
Taxon	No. individuals (% of community)	FFG*	No. individuals (% of community)	FFG*
Chironomidae	4530 (46%)	primarily CG (CG/SHH – late instar larvae)	1743 (57%)	primarily CG (CG/SHH – late instar larvae)
Zooplankton	3720 (38%)	CF (40%), pred (60%)	297 (10%)	CF (71%), pred (29%)
Oligochaeta	886 (9%)	CG	474 (16%)	CG
Trichoptera	593 (6%)	CF (55%), CF/SHH/pred (41%), CG/SHH (< 1%), PH/scr (2%)	416 (14%)	CF (86%), CF/SHH/pred (8%), PH/scr (6%)
Hydra	47 (< 1%)	Pred	74 (2%)	pred
Total	9776 (99%)	Primarily collectors	3004 (99%)	Primarily collectors
Other	<1 %	Primarily CG, followed by pred	<1%	Primarily CF, followed by CG

Site N days 2-30 (n = 36)		
Taxon	No. individuals (% of community)	FFG*
Zooplankton	531 (22%)	CF (11%), pred (89%)
Chironomidae	492 (20%)	Primarily CG
Oligochaeta	377 (15%)	CG
Ephemeroptera	306 (12%)	CG/scr (97%), CG (3%)
Trichoptera	278 (11%)	CF (59%), CG/SHH (27%), SHH (3%), CF/SHH/pred (11%), CF/scr (< 1%)
Simulidae	142 (6%)	CF
Amphipoda	99 (4%)	CG (possible SH)
Isopoda	72 (3%)	CG (possible SH)
Plecoptera	53 (2%)	CG/pred
Total	2350 (95%)	Primarily collectors
Other	4%	Primarily pred, followed by CG

* FFG = Functional Feeding Group for aquatic insects from Merritt and Cummins (1996): collector-filterer (CF), collector-gatherer (CG), scraper (scr), Shredder-herbivore (SHH), predator (pred), piercer-herbivore (PH)

Table 5. Species richness at sites SB (upstream) and N (downstream).

	No. species					
	Days 2-30 (n = 36)			Day 60 (n = 7)	Days 2-60 (n = 43)	
Taxon	SB	N	SB + N	SB	SB	SB + N
Chironomidae	19	51	54	20	26	58
Other Diptera	3	7	8	2	3	8
Ephemeroptera	2	5	5	1	2	5
Plecoptera	1	1	1	1	1	1
Trichoptera	7	8	10	6	9	11
Coleoptera	5	4	6	0	5	6
Hemiptera	1	2	2	0	1	2
Other insect genera	1	4	4	0	1	4
Arachnida	1	3	3	0	1	3
Zooplankton	5	6	6	3	5	6
Other Crustacea	2	3	3	1	2	3
Oligochaeta	2	2	2	2	2	2
Other non-insects	2	3	3	1	2	3
Total	52	102	110	37	60	115

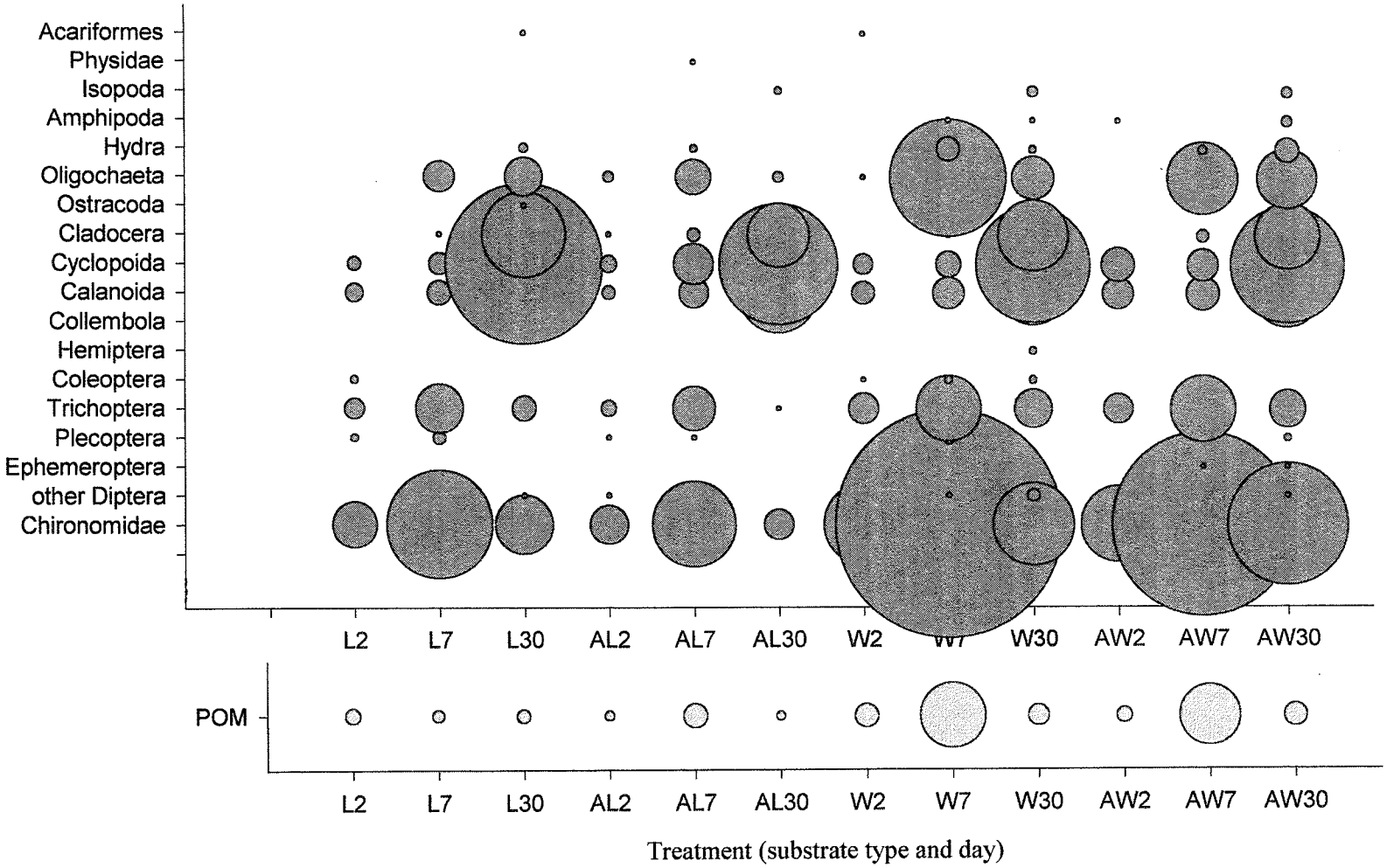


Figure 5. Site SB: Comparison of invertebrate abundance and accumulated particulate organic matter (POM). Circle size is proportional to total number of individuals and accumulated POM dry mass (g) collected from substrates L (leaf packs), AL (artificial leaf packs), W(wood), and AW (artificial wood) on days 2, 7, and 30. Individual taxa range from a mean of 0-534 individuals. POM ranges from a mean of 0.08-3.77 g.

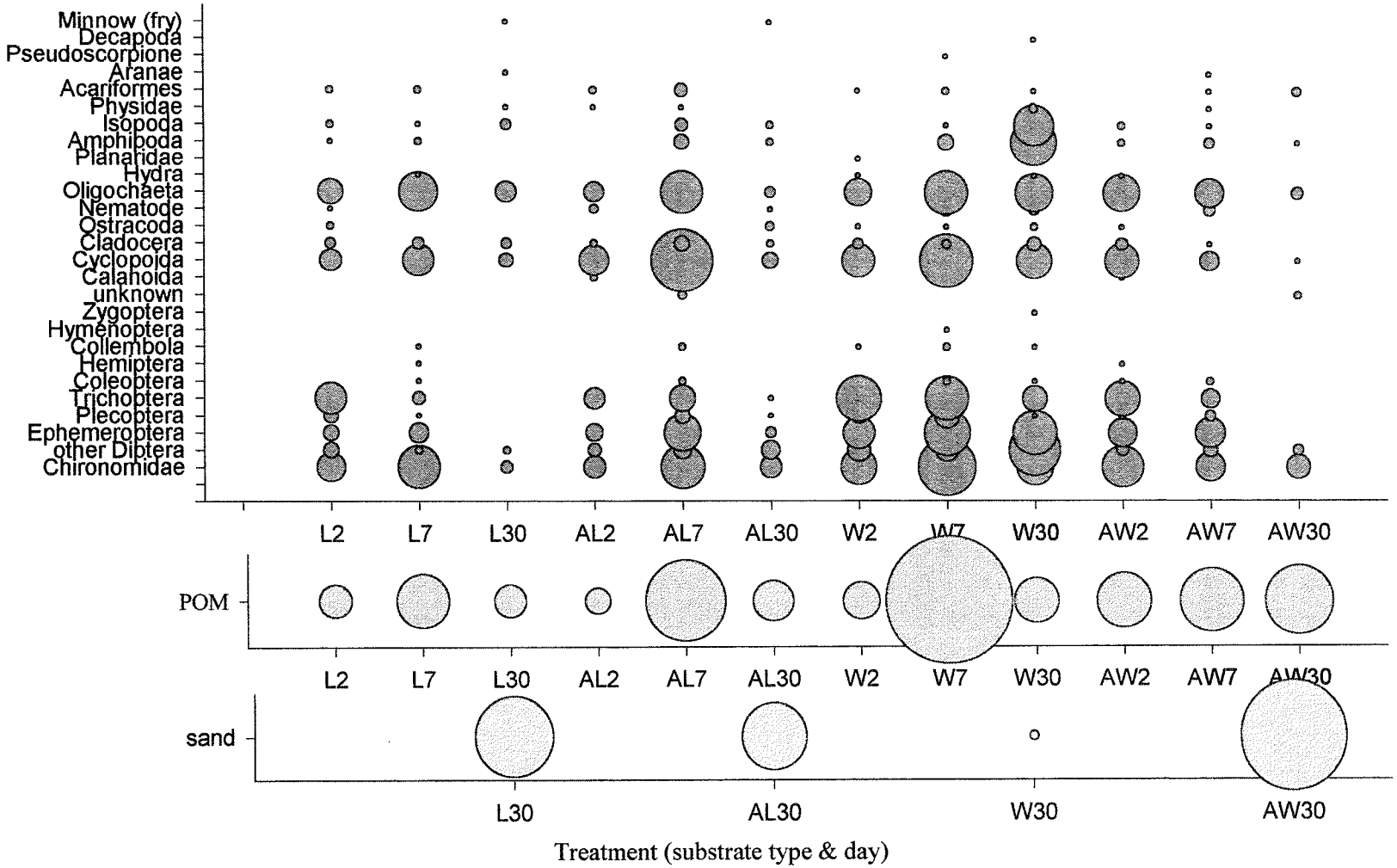


Figure 6. Site N: Comparison of invertebrate (and minnow) abundance, accumulated POM, and sand. Circle size is proportional to total number of individuals and accumulated POM and sand dry mass (g) from substrates L (leaf pack), AL (artificial leaf pack), W (wood), and AW (artificial wood) on days 2, 7, and 30; sand was measured on day 30 only. Individual taxa range from a mean of 0-42 individuals. POM ranges from a mean of 0.6-14.4 g. Sand ranges from a mean of 1.0-122.5 g.

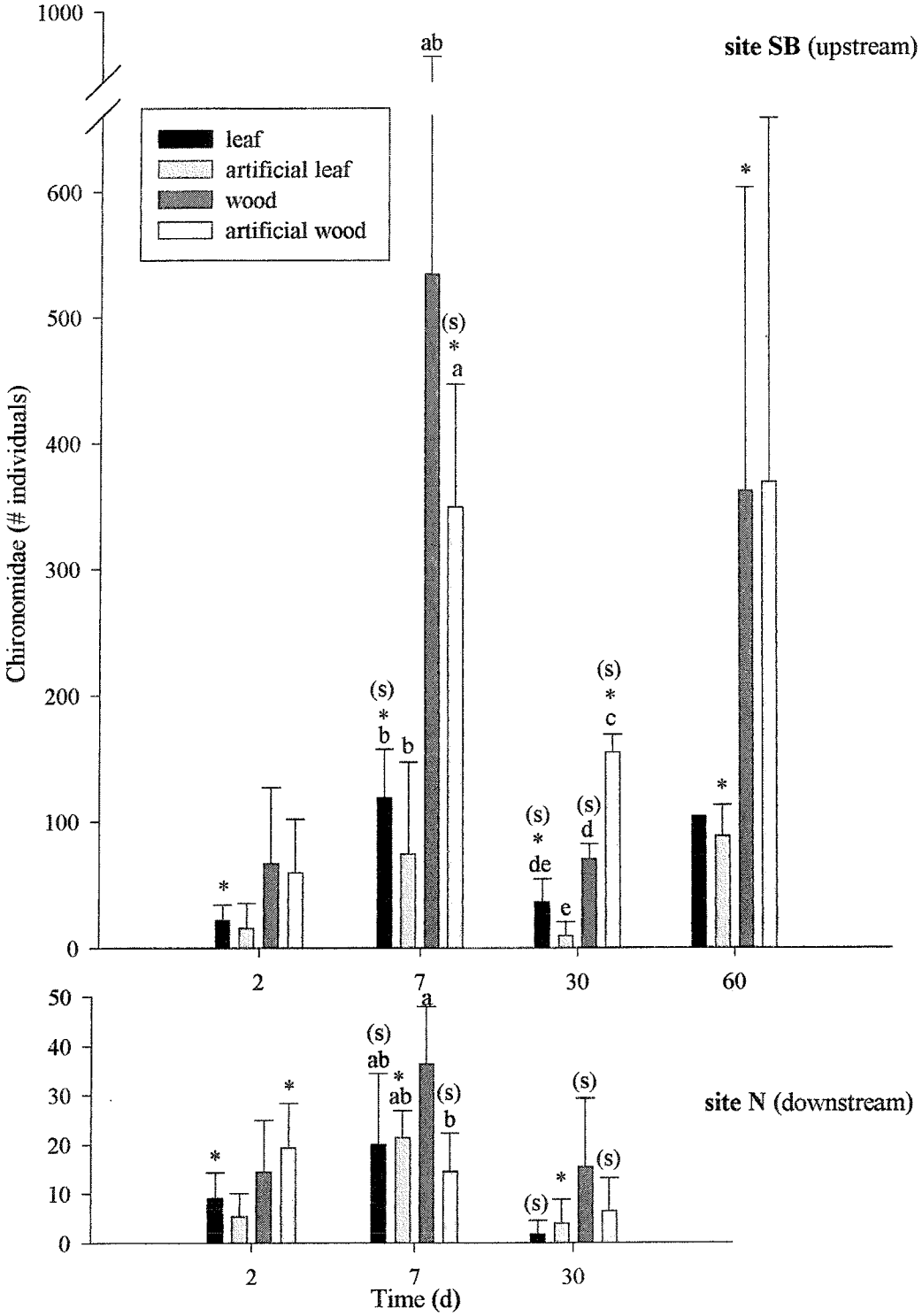


Figure 7. Mean chironomid abundance (+ SD) versus time (d) for sites SB and N. Letters denote significant substrate effects within a site and period of time. An * denotes a significant increase or decrease in abundance between sampling periods, within a site. (s) denotes a significant difference between sites, within a period of time. N = 3 on days 2-30, n = 2 on day 60 for all but leaf (n = 1).

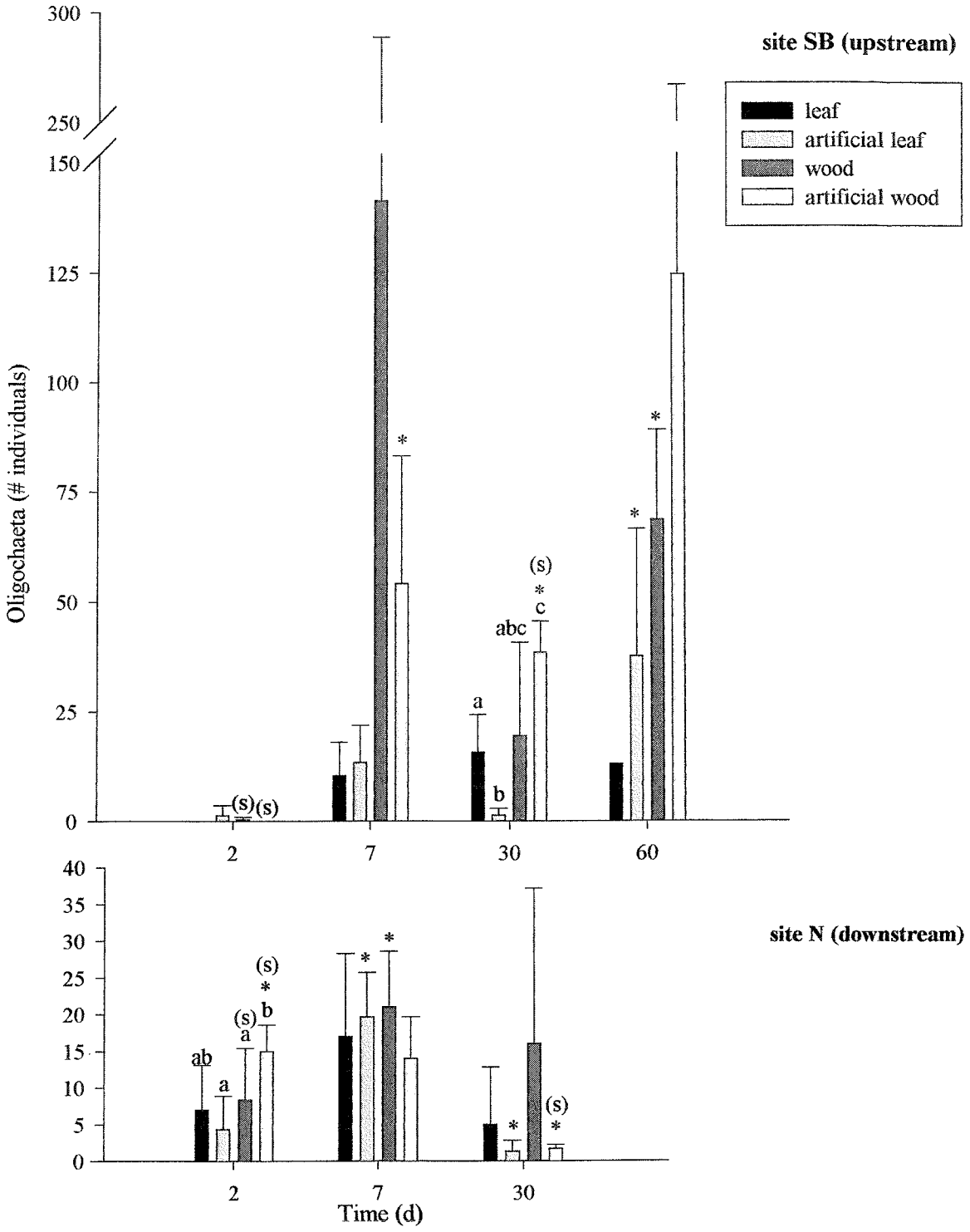


Figure 8. Mean oligochaete abundance (+ SD) versus time (d) for sites SB and N. Letters denote significant substrate effects within a site and period of time. An * denotes a significant increase or decrease in abundance between sampling periods, within a site. (s) denotes a significant difference between sites, within a period of time. N = 3 on days 2-30, n = 2 on day 60 for all but leaf (n = 1).

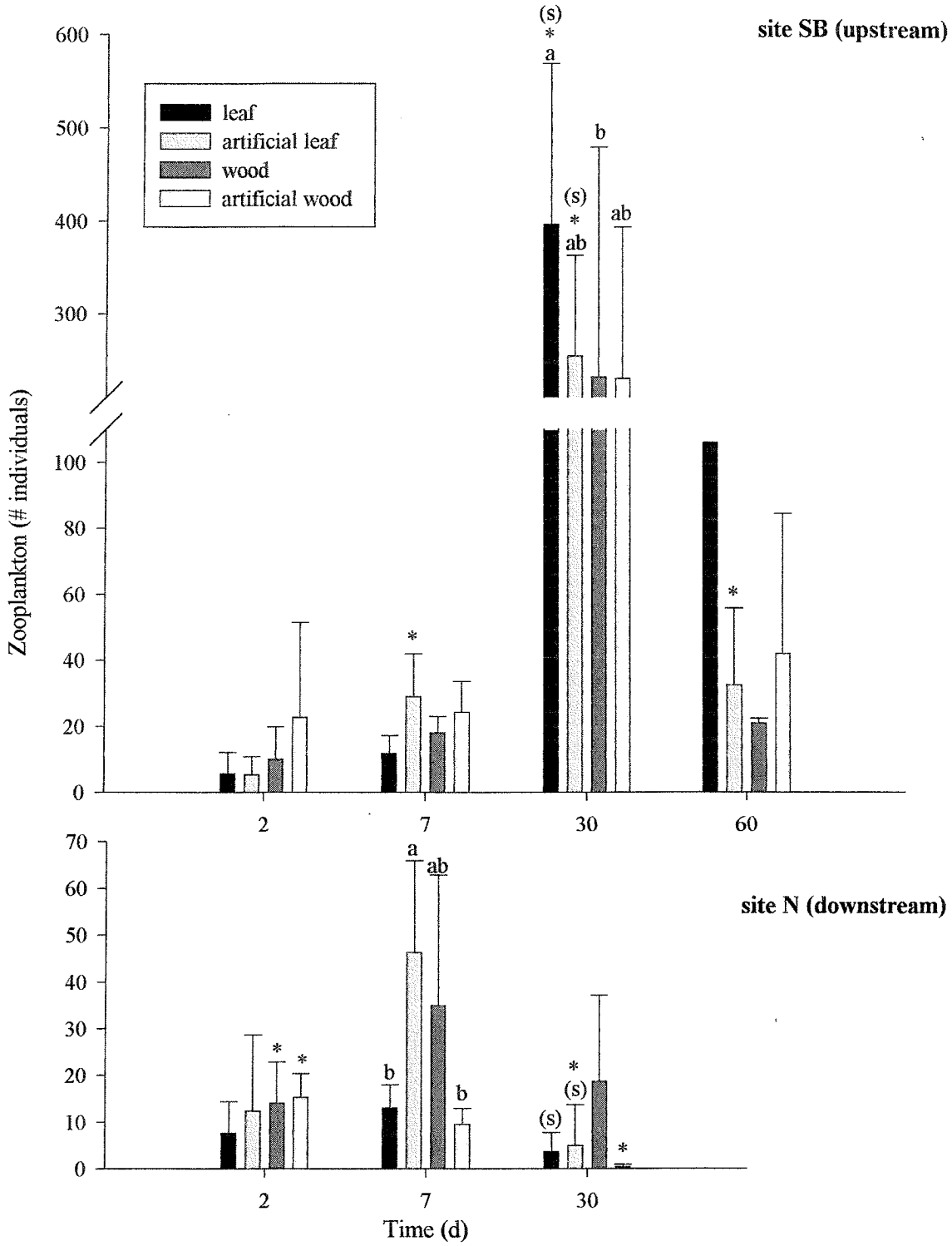


Figure 9. Mean zooplankton abundance (+ SD) versus time (d) for sites SB and N. Letters denote significant substrate effects within a site and period of time. An * denotes a significant increase or decrease in abundance between sampling periods, within a site. (s) denotes a significant difference between sites, within a period of time. N = 3 on days 2-30, n = 2 on day 60 for all but leaf (n = 1).

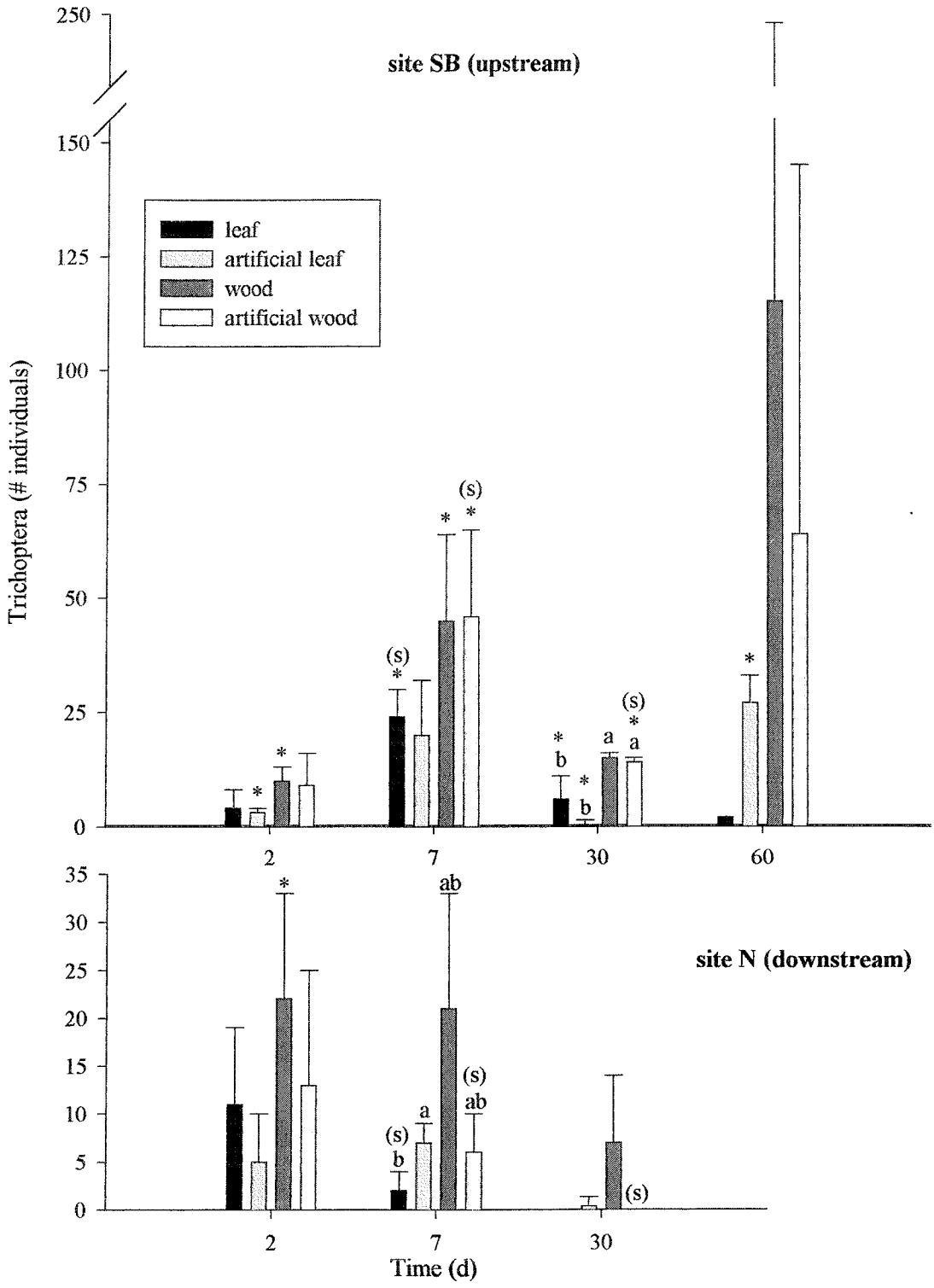


Figure 10. Mean trichopteran abundance (+ SD) versus time (d) for sites SB and N. Letters denote significant substrate effects within a site and period of time. An * denotes a significant increase or decrease in abundance between sampling periods, within a site. (s) denotes a significant difference between sites, within a period of time. N = 3 on days 2-30, n = 2 on day 60 for all but leaf (n = 1).

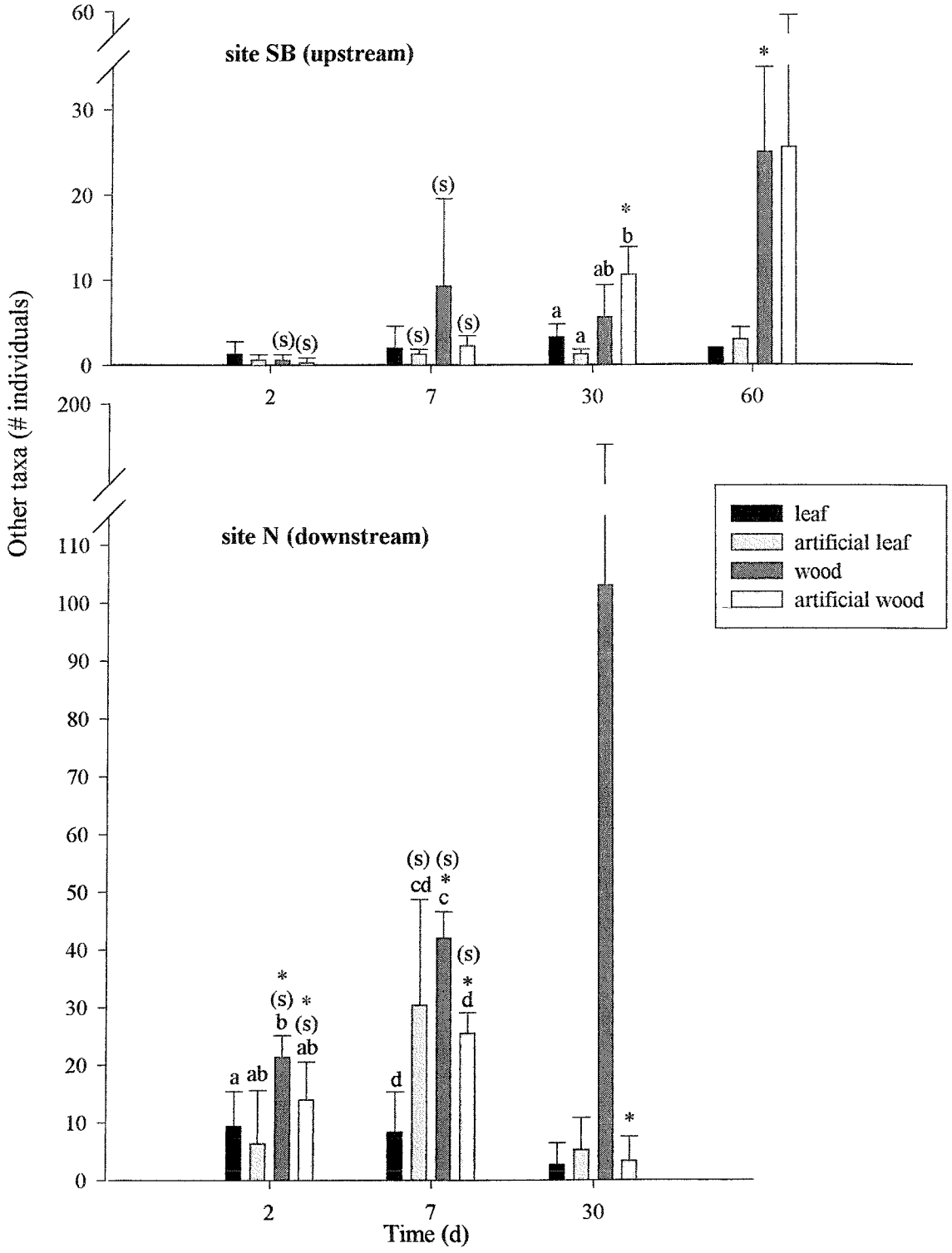


Figure 11. Mean abundance (+ SD) of remaining taxa versus time (d) for sites SB and N. Letters denote significant substrate effects within a site and period of time. An * denotes a significant increase or decrease in abundance between sampling periods, within a site. (s) denotes a significant difference between sites, within a period of time. N = 3 on days 2-30, n = 2 on day 60 for all but leaf (n = 1).

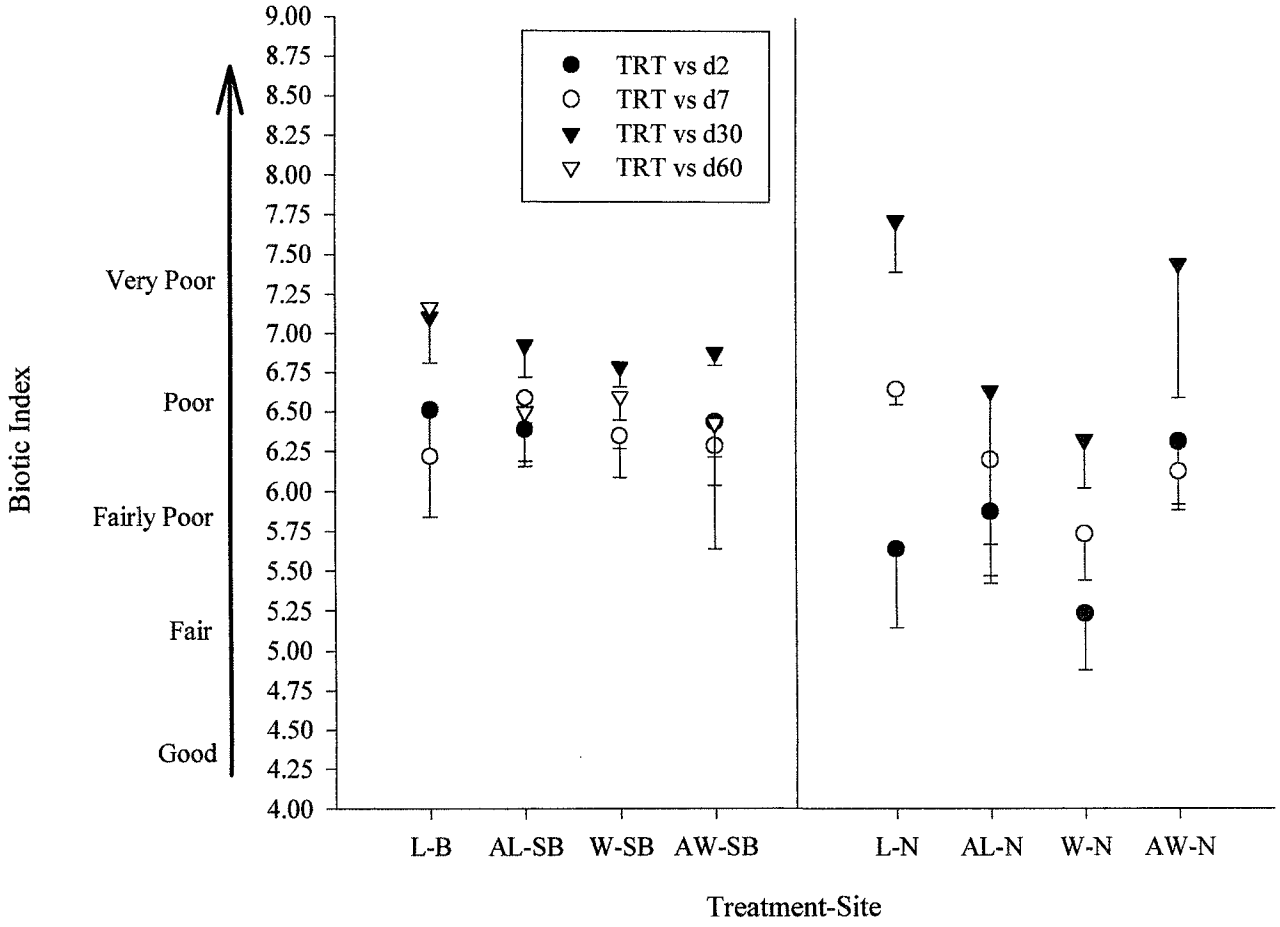


Figure 12. Biotic indices for invertebrates colonizing substrates L (leaf pack), AL (artificial leaf pack), W (wood), AW (artificial wood), at sites SB and N, on days 2, 7, 30 and 60.

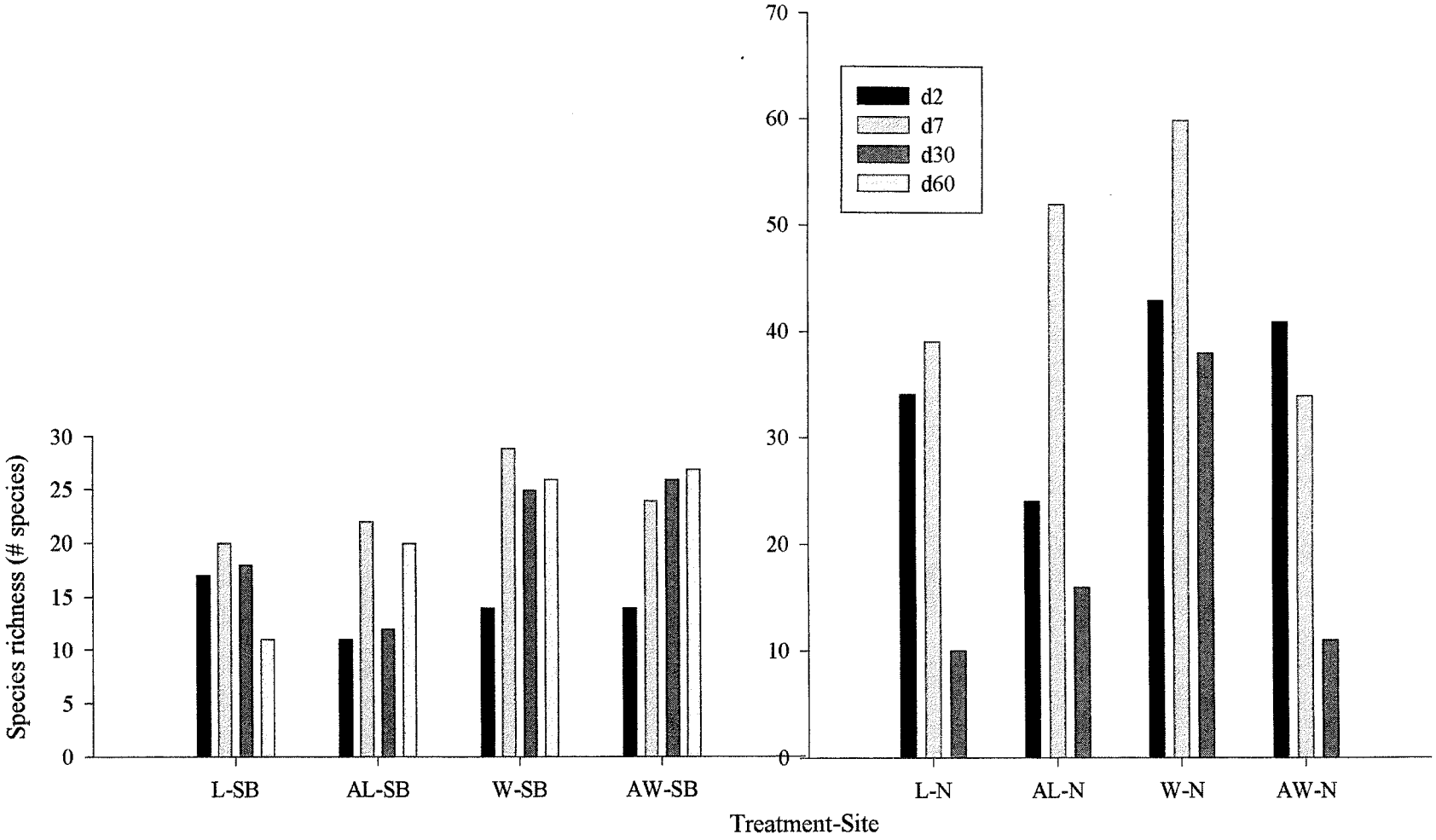


Figure 13. Species richness at sites SB (upstream) and N (downstream), from substrates L (leaf packs), AL (artificial leaf packs), W (wood), and AW (artificial wood) on days 2, 7, 30, and 60. Zooplankton are included. Replicates from each substrate type, site, and date were pooled for each treatment.

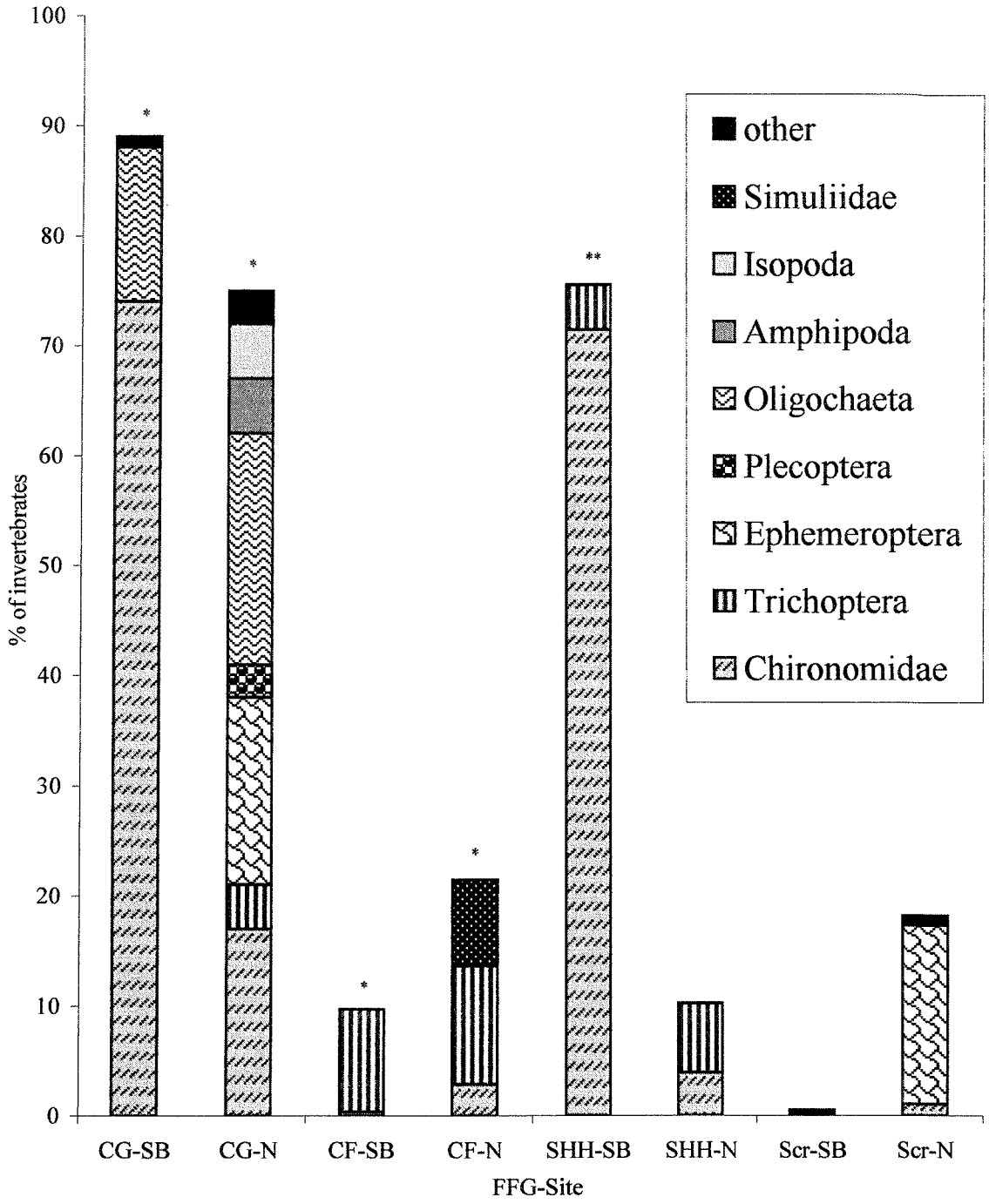


Figure 14. Relative abundance (%) of invertebrates within Functional Feeding Groups (FFG) from sites SB and N. Values represent the proportion of total invertebrates collected on days 2, 7, and 30. Individuals with multiple feeding modes were placed in more than one category. FFGs not depicted were similar between sites. *When zooplankton are included, CG and CF become more similar between sites, in terms of relative abundance. **SB SHH represents feeding potential; Cricotopus spp. (Chironomidae) were not functioning as SHH at SB, and thus SHH was similar between sites. CG = collector-gatherer, CF = collector-filterer,
SHH = shredder-herbivore, Scr = scraper

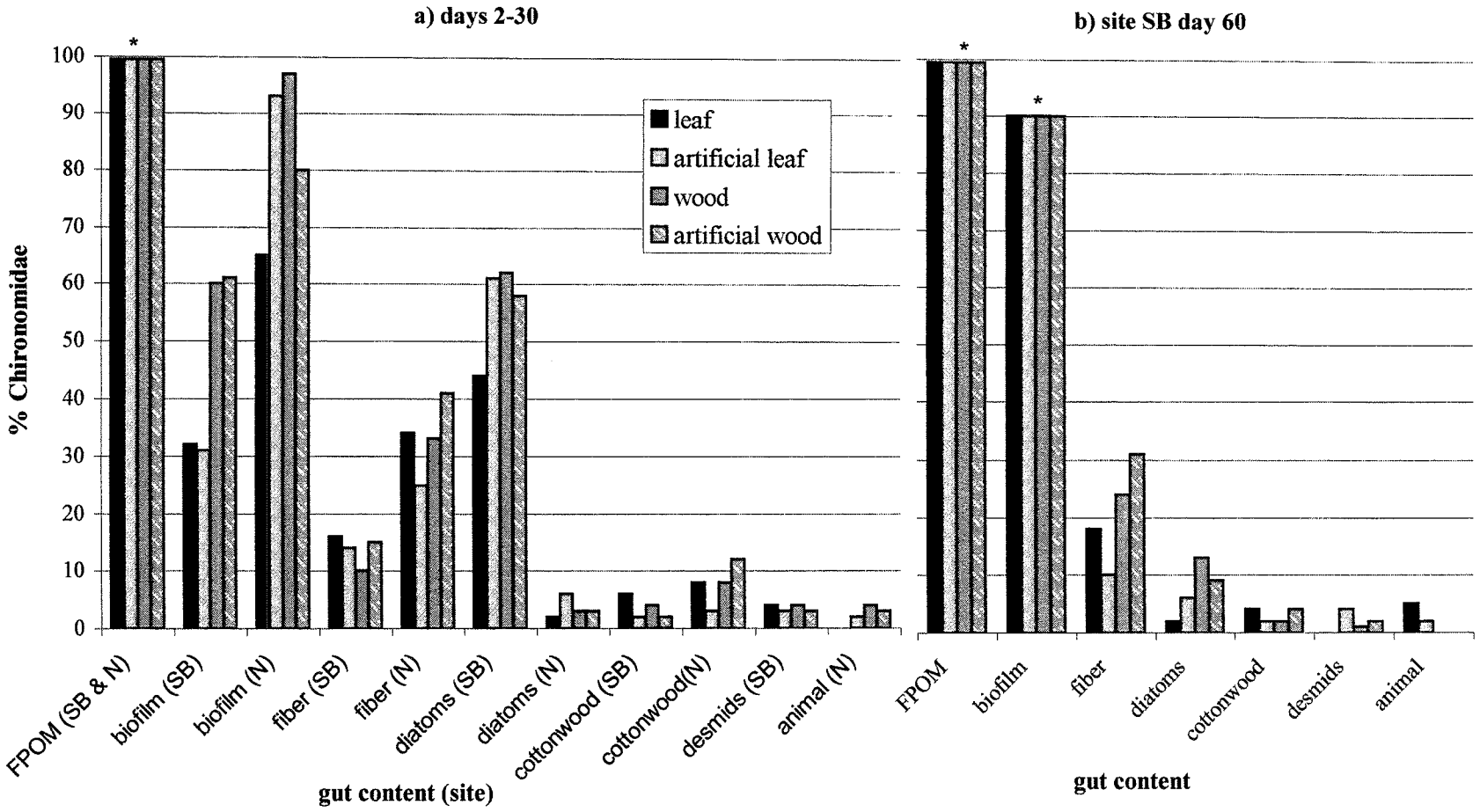


Figure 15. Relative abundance (%) of Chironomidae larvae that contained specific gut contents from leaf and wood substrates at sites SB (upstream) and N (downstream). Values represent total percent of larvae from a) days 2-30 and b) day 60 site SB. Data resulting in < 1% of larvae are not presented. * FPOM occurred in essentially all larvae and was estimated at 99.5%. At least 90% of larvae were estimated to contain biofilm from SB d60 substrates.

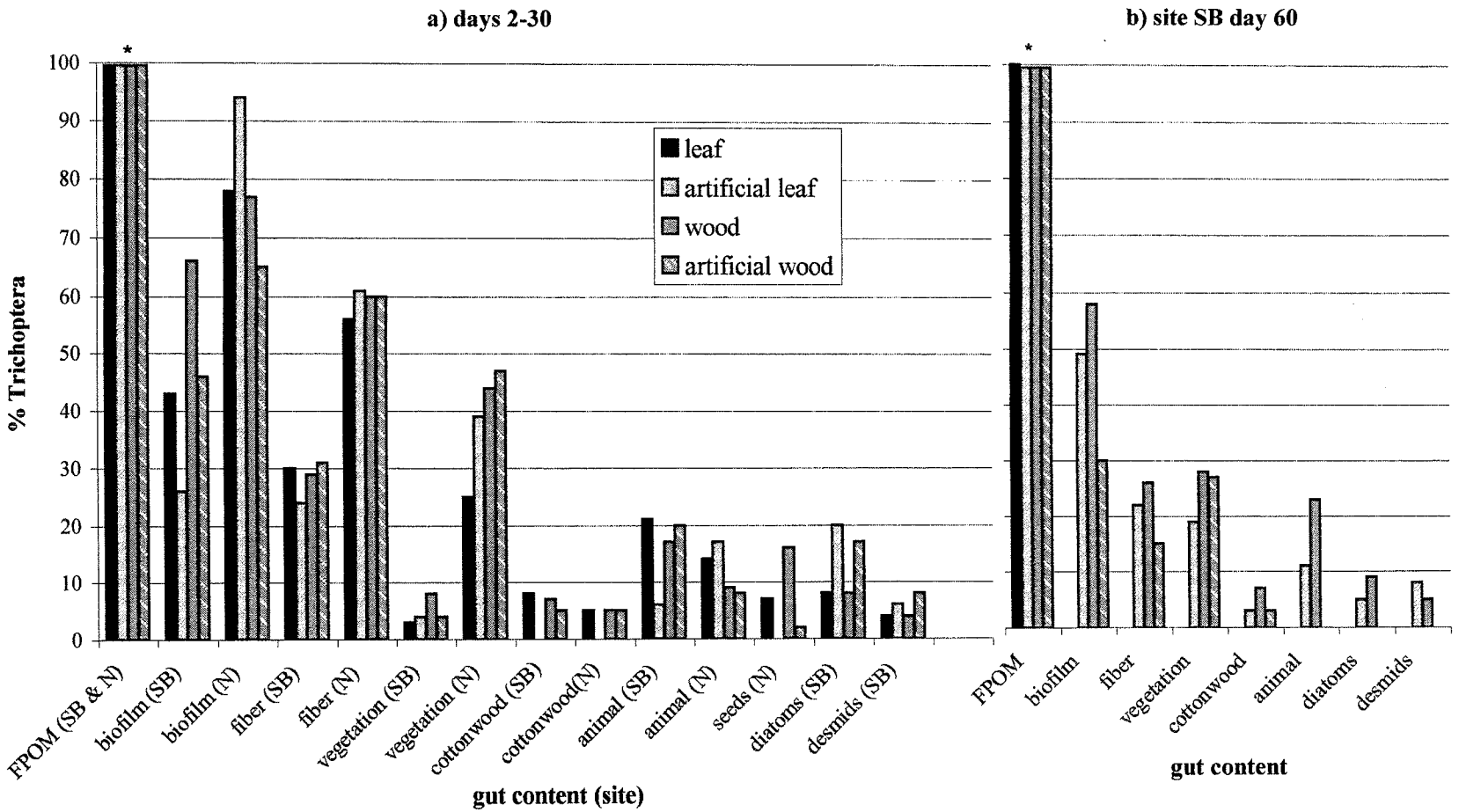


Figure 16. Relative abundance (%) of Trichoptera larvae that contained specific gut contents from leaf and wood substrates at sites SB (upstream) and N (downstream). Values represent total percent of larvae from a) days 2-30 and b) day 60 site SB. Data resulting in < 1% of larvae are not presented. *FPOM occurred in essentially all larvae and was estimated at 99.5%; the exception was leaf at SB d60 where only two larvae were collected, each with very little FPOM only.

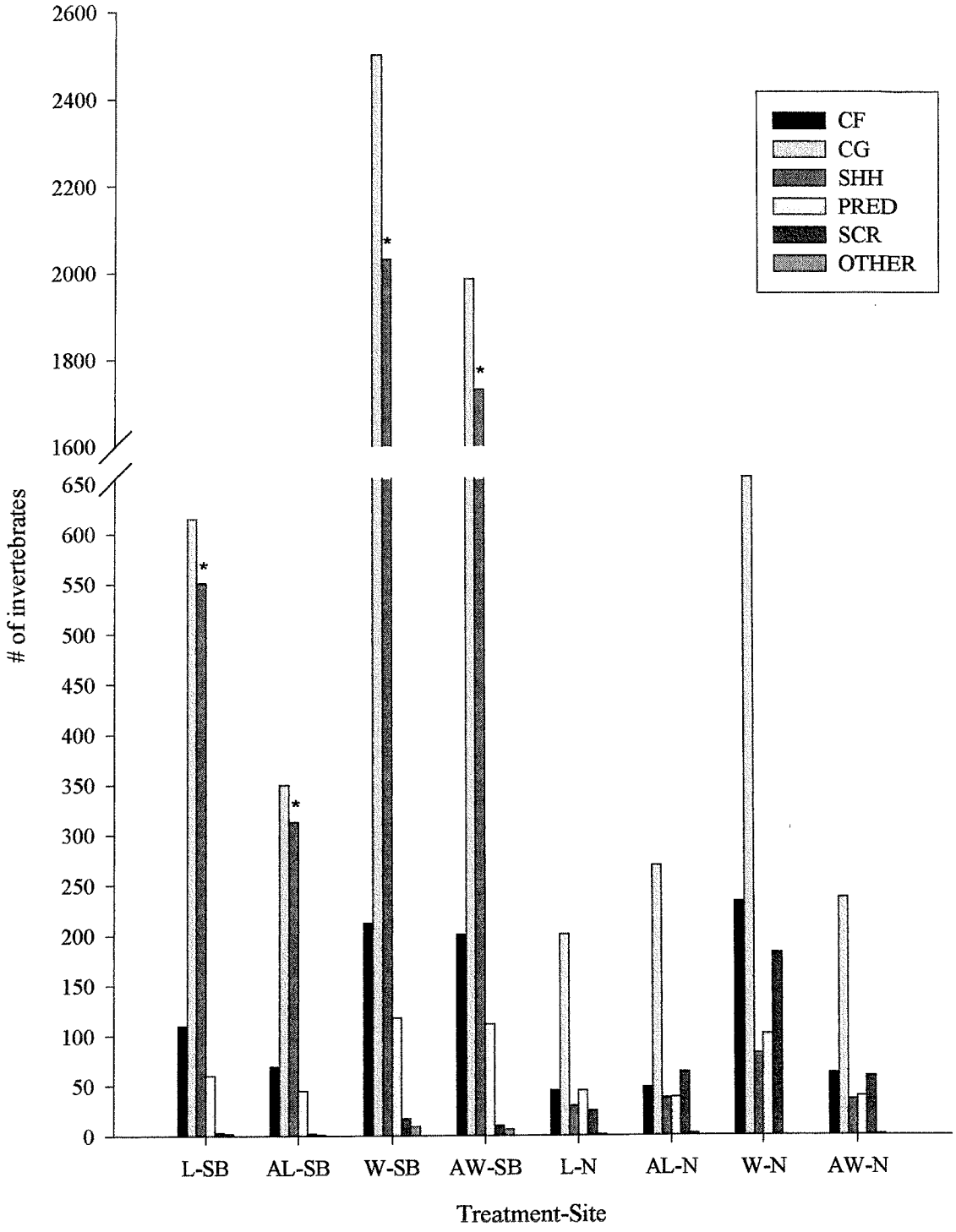


Figure 17. Effects of site (SB, N) and substrate (L, AL, W, AW) on trophic relationships in terms of maximum abundance of invertebrates within functional feeding groups. Data from days 2, 7, and 30 combined. Zooplankton were not included in these data.
*Represents SHH potential; actual SHH feeding was similar to that of site N.

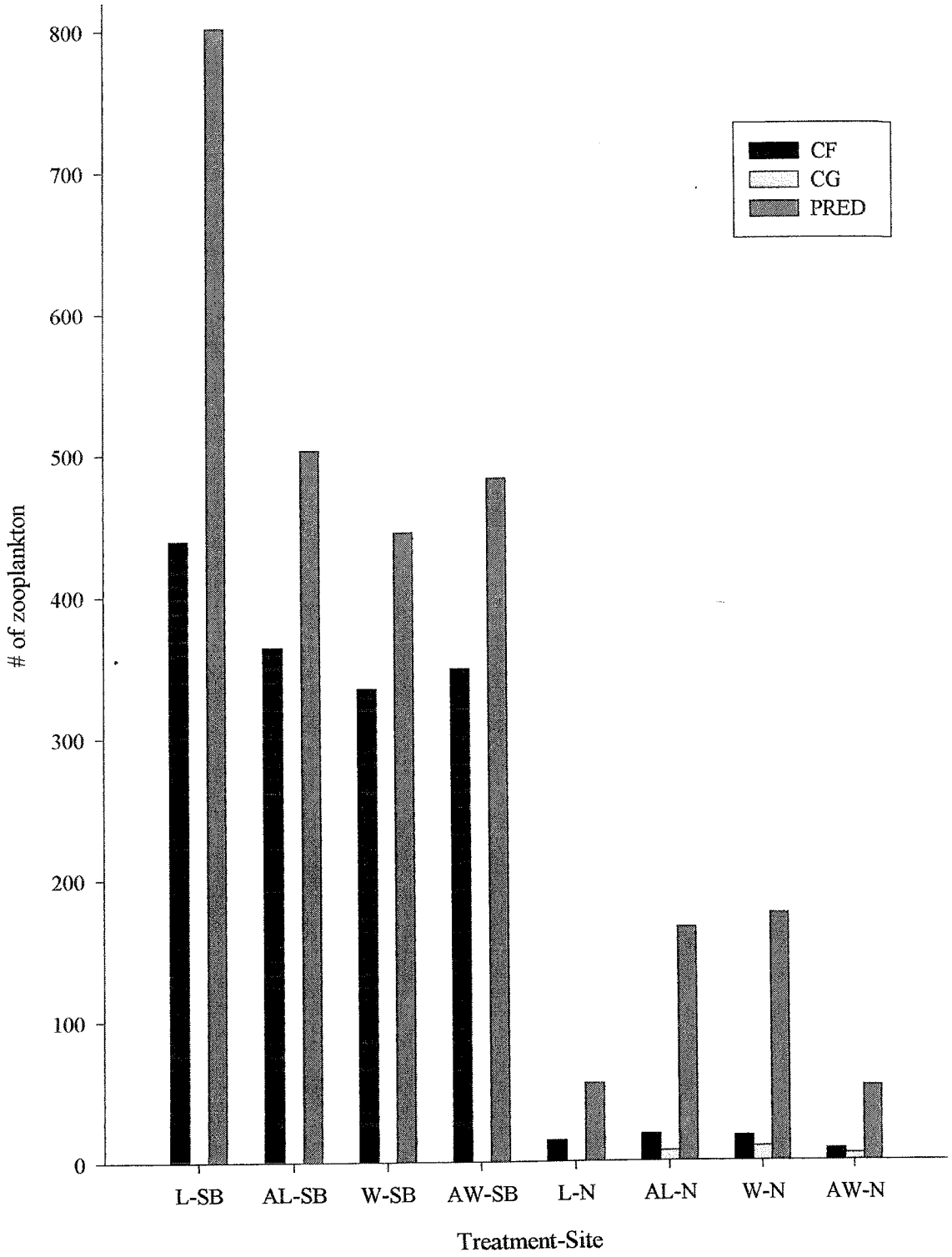


Figure 18. Effects of site (SB, N) and substrate (L, AL, W, AW) on trophic relationships in terms of maximum abundance of zooplankton within functional feeding groups. Data from days 2, 7, and 30 combined.

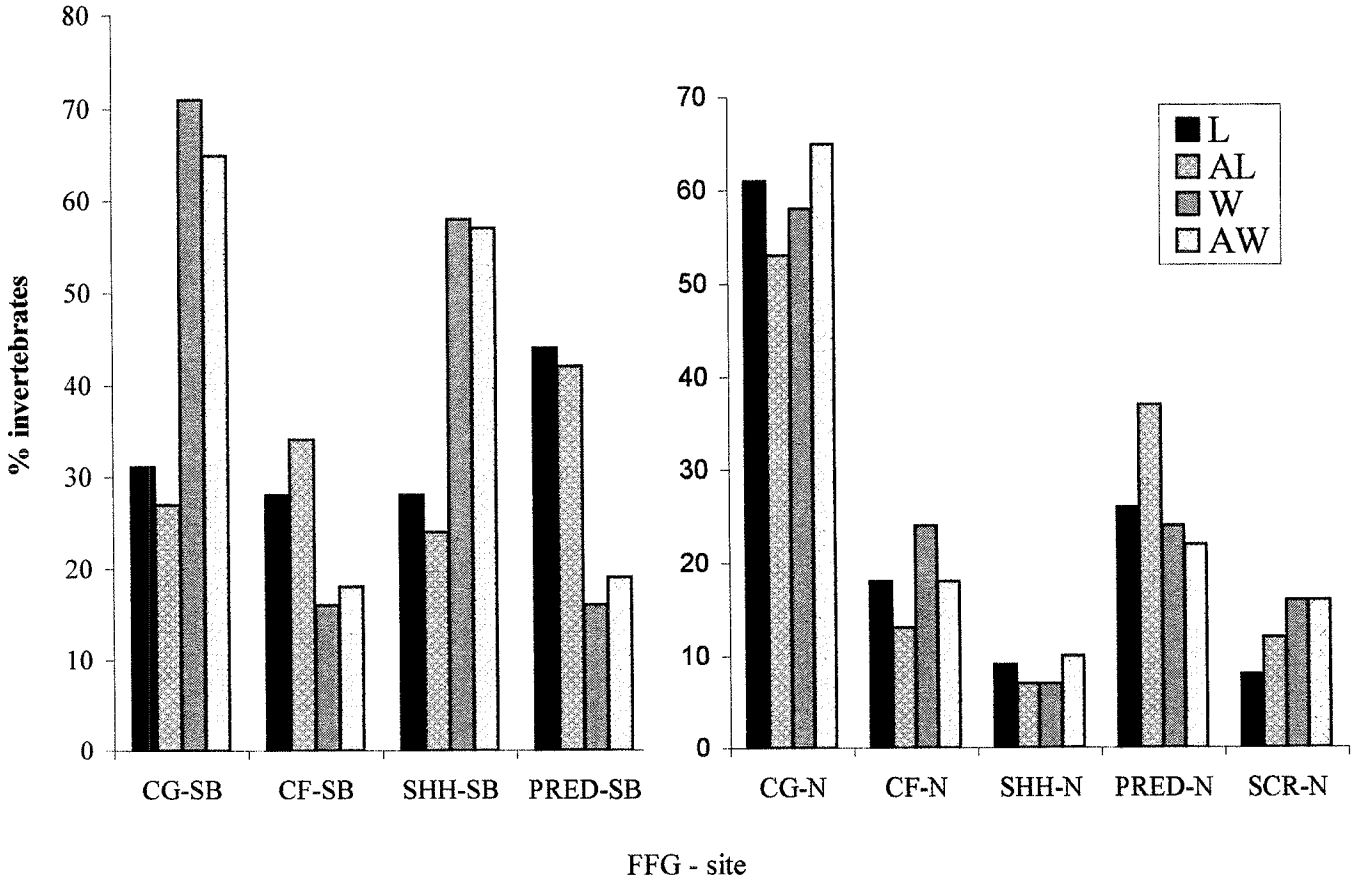


Figure 19. Effects of site (SB, N) and substrate (L, AL, W, AW) on trophic relationships in terms of maximum relative abundances (%) of invertebrates within functional feeding groups (FFG). Data from days 2, 7, and 30 were combined. Zooplankton were included in these data. For site SB, when zooplankton were omitted from the data, differences were < 10%.

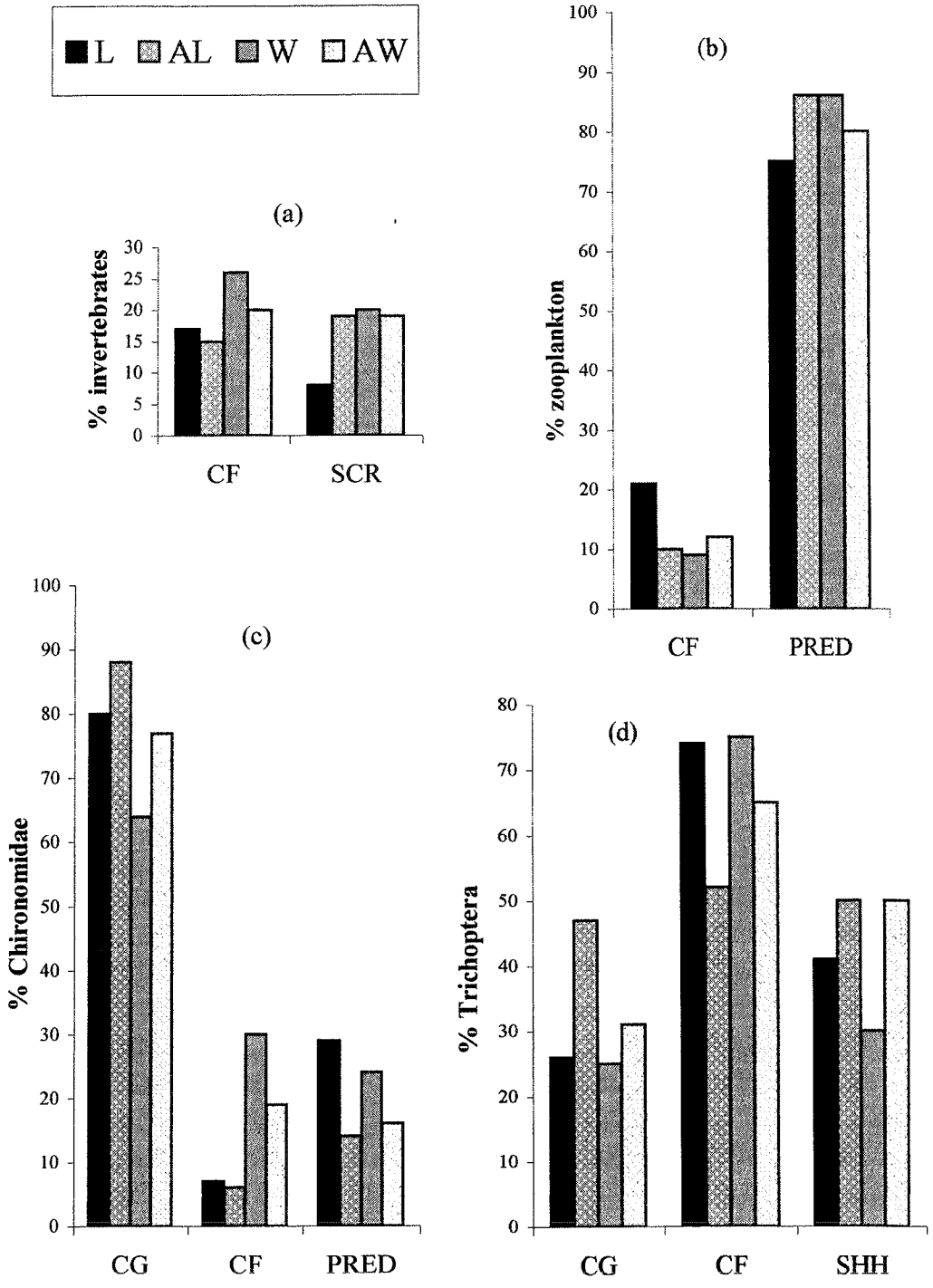


Figure 20. Trophic Relationships (substrate effects) at site N in terms of maximum relative abundance of a) invertebrates, with zooplanktin omitted, b) zooplankton, c) Chironomidae, and d)Trichoptera within functional feeding groups (FFG).

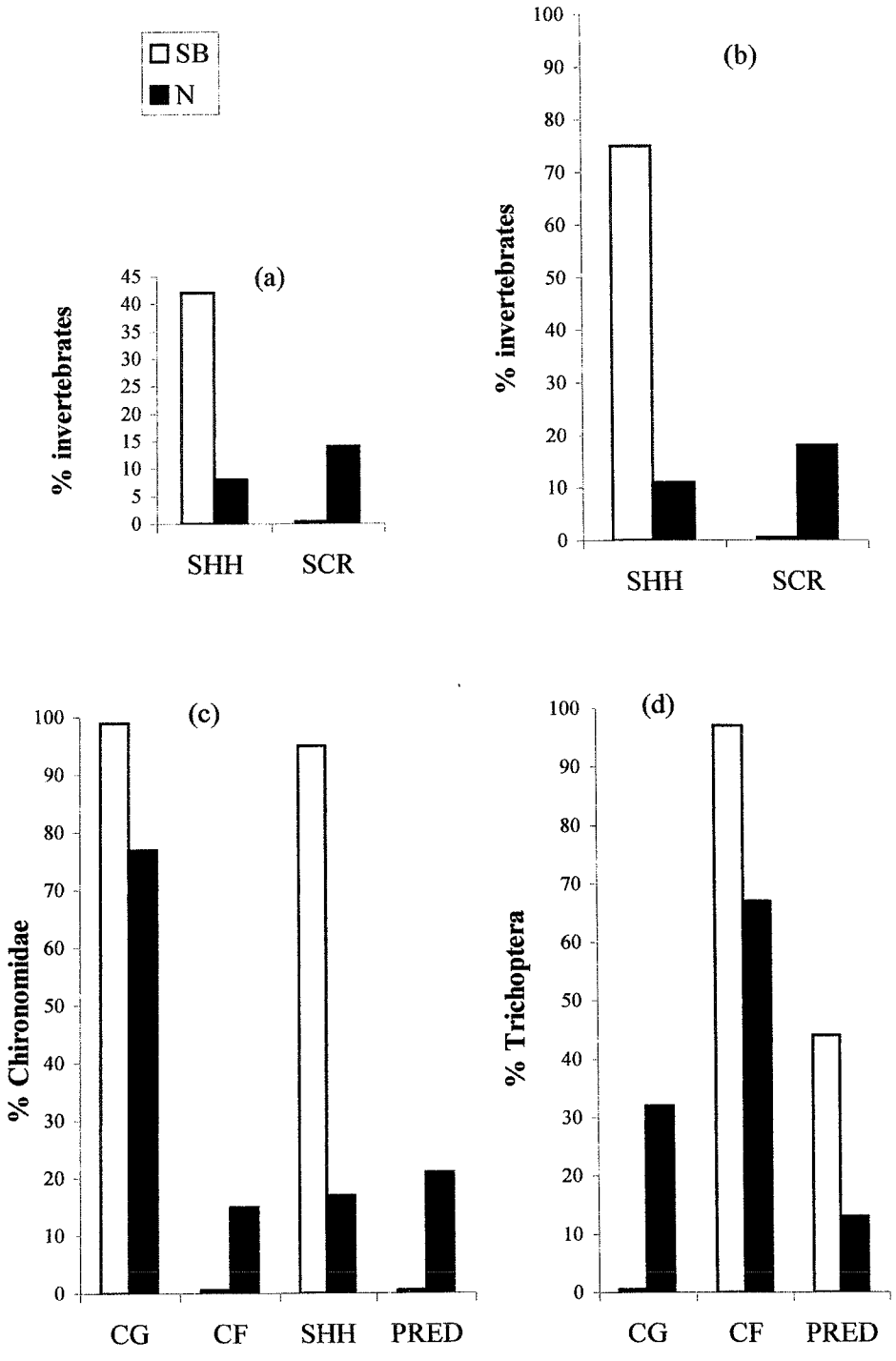


Figure 21. Effects of site (SB, N) on trophic relationships in terms of maximum relative abundance (%) of functional feeding groups (FFG) for a) invertebrates, b) invertebrates, with zooplankton omitted, c) Chironomidae, and d) Trichoptera.

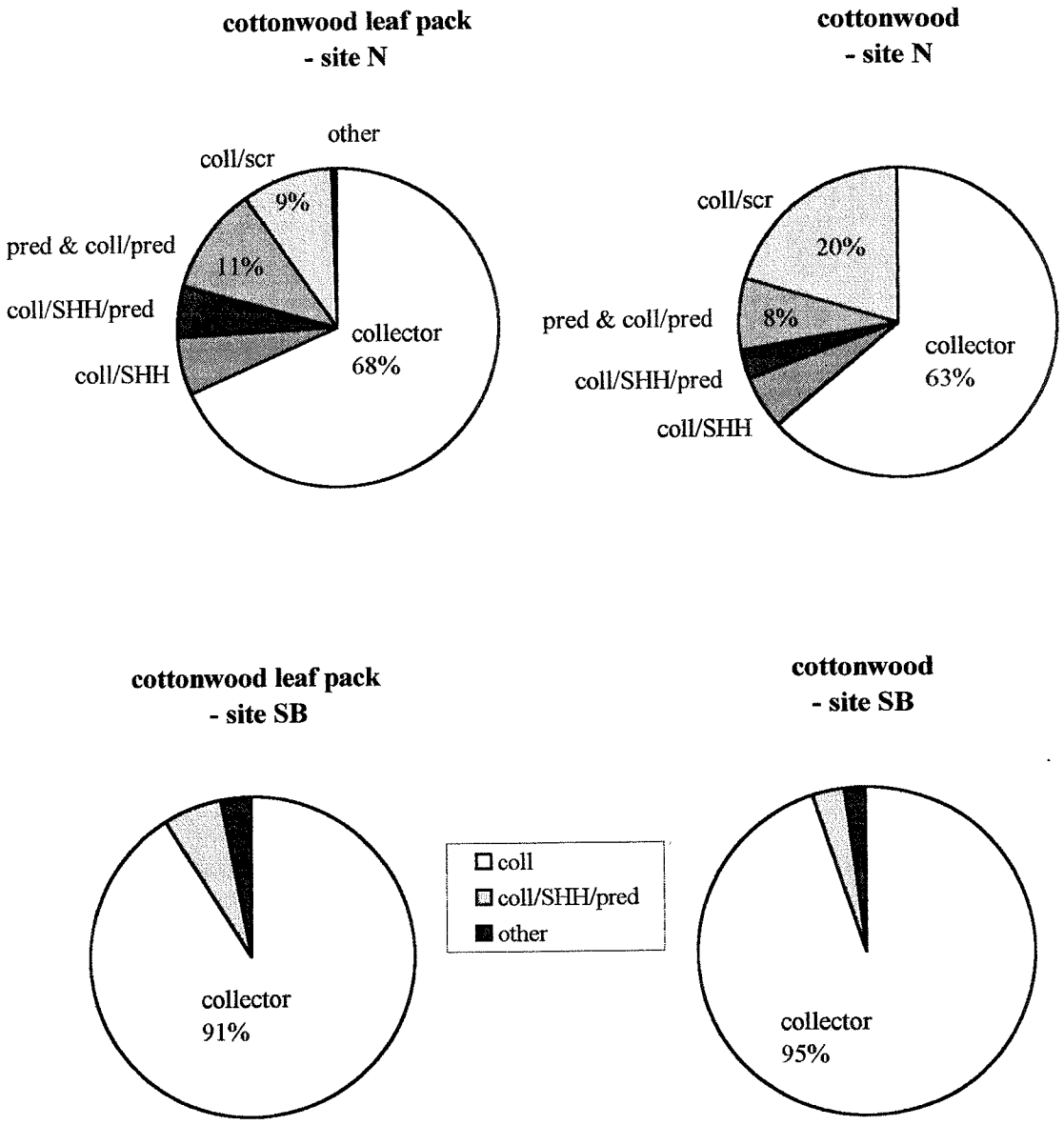


Figure 22. Relative abundance (%) of the functional feeding groups as described by Merritt and Cummins (1996) and Vannote et al. (1980); coll = collector, SHH = shredder/herbivore, pred = predator, and scr = scraper. Many taxa have multiple feeding modes. Data were combined from days 2, 7, and 30 for cottonwood leaf packs and wood substrates of sites SB and N. Zooplankton were omitted from these data.

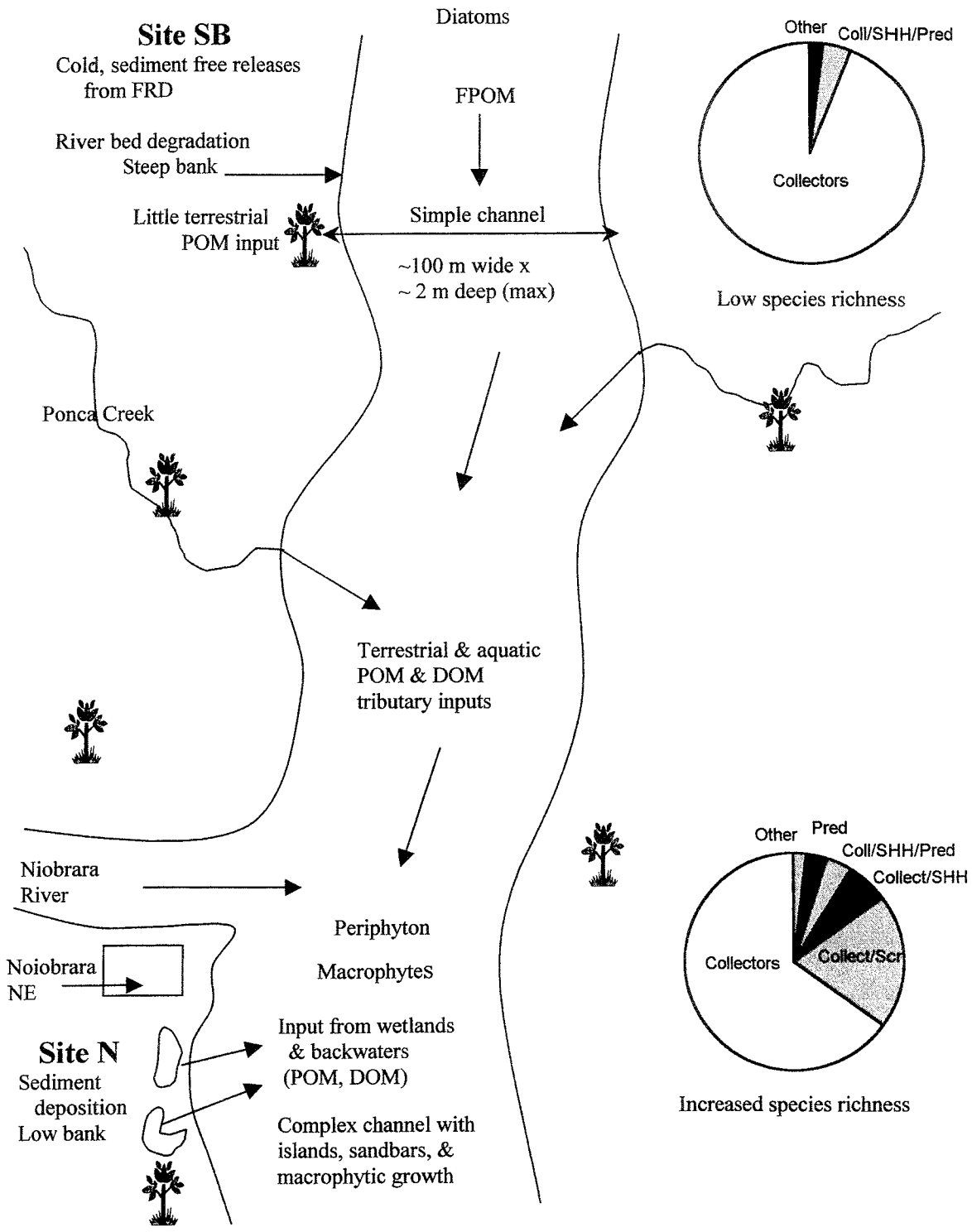
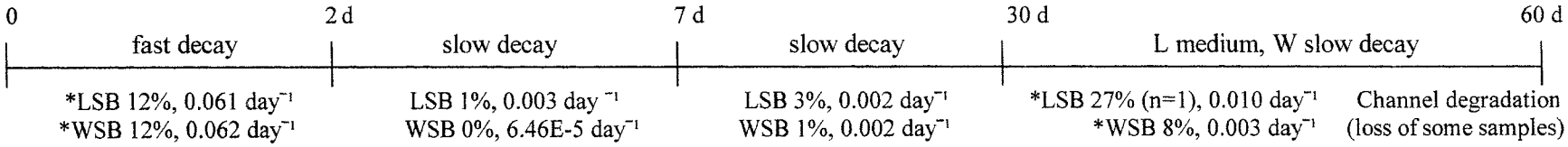


Figure 23. Inferred structure and function of an unchannelized reach of the Missouri River, from May-June, between Fort Randal and Gavins Point Dams. Includes field sites SB and N of this study. Fort Randall Dam (FRD) is approximately 50 km upstream from site SB.

2.6.1. Appendix

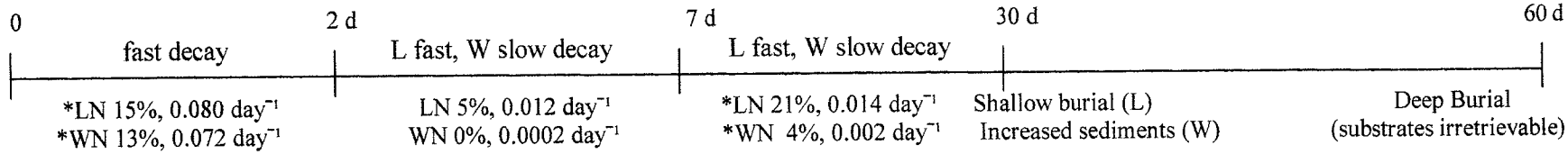
Time line (summary results)

a) Upstream (SB)



Biotic Index:	Fairly Poor (L & W)	Fairly Poor (L & W)	Poor (L & W)	Poor (L & W)
Temperature:	8°C	8°C	11.5°C	19°C
Velocity:	19(4) cm/s		14(9) cm/s	Increased Velocity
POM:	L 0.23 g, W 0.49 g	L 0.13 g, W 3.76 g	L 0.17 g, W 0.40 g	
Tl Invertebrates:	L 33(13), W 88(69)	L 167(43), W 748(598)	L 458(149), W 342(227)	L 227(n=1), W 591(344)
Species richness:	L 9(1), W 9(2)	L 14(3), W 20(2)	L 14(2), W 17(3)	L 11(n=1), W 21(1)

b) Downstream (N)



Biotic Index:	Fair (L & W)	Poor (L), Fairly Poor (W)	Very Poor (L), Fairly Poor (W)
Temperature:	15°C	15°C	28°C
Velocity:	46(9) cm/s		38(7) cm/s
POM:	L 0.99 g, W 1.26 g	L 2.56 g, W 14.38 g	L 0.94 g, W 1.76 g
Tl Invertebrates:	L 44(28), W 80(25)	L 60(37), W 155(38)	L 13(19), W 160(140)
Species richness:	L 19(7), W 23(4)	L 19(11), W 35(6)	L 4(4), W 20(15)

Figure 1: Time line in days (d) for cottonwood leaves (L) and wood (W) at field sites SB & N. Mean mass loss (%), breakdown rates (k-values = day^{-1}), and "water quality" as indicated by biotic index values from substrates are included. Asterics indicate significant mass loss within the time period. In addition, water temperature, mean (sd) current velocity experienced by the substrates, and mean accumulated POM dry mass are included since they should influence the values. Invertebrate colonization is also listed in terms of mean (sd) abundance and species richness.

2.6.2. Appendix A

Leaf and Wood Decomposition

Table 1. Mean leaf (L) and wood (W) mass loss in grams (± SD), at sites SB (upstream) and N (downstream). Initial dry mass was approximately 4 g for L, and 66 g for W. Final ash free dry mass (AFDM) of L is also included.

Trt-site	Day	No. reps. recovered	Final dry mass (g)	Mass loss (g)	AFDM (g)
L-SB	2	3	3.54 (0.04)	0.46 (0.04)	3.21 (0.03)
	7	3	3.48 (0.12)	0.52 (0.12)	3.13 (0.12)
	30	3	3.35 (0.08)	0.65 (0.08)	2.62 (0.14)
	60	1	2.27	1.73	1.93
L-N	2	3	3.41 (0.12)	0.59 (0.12)	3.36 (0.12)
	7	3	3.21 (0.16)	0.79 (0.16)	2.91 (0.15)
	30	3	2.34 (0.28)	1.66 (0.28)	2.03 (0.28)
	60	0			
W-SB	2	3	55.63 (1.32)	7.41 (0.90)	*
	7	3	62.00 (7.89)	8.83 (1.21)	*
	30	3	61.96 (6.44)	8.86 (0.11)	*
	60	2	49.98 (2.64)	13.17 (0.21)	*
W-N	2	3	54.94 (4.45)	8.49 (1.27)	*
	7	3	57.72 (9.21)	8.86 (1.66)	*
	30	3	51.70 (3.55)	10.87 (1.42)	*
	60	0			

* = missing data

Table 2. ANOVA for effects of substrate, time and site on the decomposition of leaf packs (L) and wood (W) (% mass loss), at sites SB (upstream) and N (downstream).

Substrate effects				Time effects (d)				Site effects			
site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
SB	60	L > W	*0.00	SB	L	d2 > d0	0.00	30	L	N > SB	0.00
						d60 > d30	*0.01	7	W	N > SB	0.05
N	7	L > W	0.05		W	d2 > d0	0.00	30	W	N > SB	0.01
	30	L > W	0.00			d60 > d30	*0.00				
				N	L	d2 > d0	0.00				
						d30 > d7	0.01				
					W	d2 > d0	0.00				
						d30 > d7	0.00				

* Substrate effects, day 60: r=1 for L-SB, and r=2 for W-SB. Another replicate of the same value was added to L for statistical analysis.

* Effects of time, day 60: 1) two replicates of the same value were added to L-SB for statistical analysis, 2) for W-SB, the mean of the other two replicates was added as a third replicate.

2.6.3. Appendix B

Invertebrates

Table 1. Invertebrates of Missouri River sites SB (upstream) and N (downstream) from leaf packs (L) artificial leaves (AL), wood (W) and artificial wood (AW).

[2]Taxa	Family	Genus	Species	[1]FFG	Substrate Days 2-60	Site SB and N
Insecta						
Diptera	Ceratopogonidae			pred, CG	AL, W, AW	SB, N
	Chaoboridae	*Chaoborus*	sp.	pred	AL	N
	Chironomidae	(see table 2)	(see table 2)	primarily CG	L, AL, W, AW	SB, N
	Culicidae			CF, CG	AL	N
	Empididae	*Hemerodromia*	sp.	pred, CG	L, AL, W, AW	SB, N
	Simuliidae	*Simulium*	*	CF	L, AL, W, AW	SB, N
	Stratiomyidae			CG	W	N
	Tipulidae	(early instar)		SHH, SHD, CG, pred	AL, AW	N
	unknown				L, W	SB, N
Ephemeroptera	Baetidae	*Baetis*	sp.	CG, scr	L, AL, W, AW	N
	Caenidae	*Caenis*	sp.	CG, scr	L, AL, W, AW	SB, N
	Heptageniidae	*Stenonema*	sp.	scr, CG	L, AL, W, AW	SB, N
	Tricorythidae	*Tricorythodes*	sp.	CG	AL, W, AW	N
	unknown				W	N
Plecoptera	Perlodidae	*Isoperla*	sp.	pred, CG	L, AL, W, AW	SB, N
Trichoptera	Brachycentridae	*Brachycentrus*	sp.	CF, scr	W	N
	Hydropsychidae	*Cheumatopsyche*	sp.	CF	AW	SB
		Hydropsyche	*bidens*	CF	W, AW	SB, N
		Hydropsyche	*orris*	CF	L, AL, W, AW	SB, N
		Hydropsyche	*simulans*	CF	L, AL, W, AW	SB, N
		Potamyia	*flava*	CF	L, AL, W, AW	SB, N
	Hydroptilidae	*Hydroptila*	spp.	PH, scr	L, AL, W, AW	SB
	Leptoceridae	*Nectopsyche*	sp.	SHH, CG, pred	L, AL, W, AW	SB, N
		Triaenodes	sp.	SHH	AL, W, AW	N
	Polycentropodidae	*Neureclipsis*	sp.	CF, SHH, pred	L, AL, W, AW	SB, N
		Polycentropus	sp.	pred, CF, SHH	AL, W, AW	SB

Insect Taxa (Table 1) 2 of 3

Taxa	Family	Genus	Species	FFG	Substrate days 2-60	Site SB and N
Coleoptera	Elmidae		(larvae & adults)	CG, scr	AL, W, AW	N
	Gyrinidae	*Dineutus*	sp. (adult)	pred	W	SB
	Haliplidae	*Peltodytes*	sp.	P, SHH, pred	W	SB
	Hydrophilidae		(larvae)	pred	W	SB
			(adult)	CG	W	SB
	Staphylinidae			pred	L, AW	SB, N
	unknown				L, W	SB, N
Hemiptera	Corixidae			CG, PH, pred, scr	W, AW	SB, N
	unknown				L	N
Hymenoptera				parasite	W	N
Zygoptera (Odonata)	Coenagrionidae			pred	W	N
Collembola	Entomobryidae?	*Sminthurides* ?		CG, SHH	L, AL, W, AW	SB, N

Non-Insect Taxa				FFG	Substrate Days 2-60	Site SB and N
Chilicerata	Arachnida	Acariformes		pred	L, AL, W, AW	SB, N
		Aranae		pred	L, AW	N
		Pseudoscorpiones		pred	W	N
Gastropoda	Physidae	*Physa*		scr, CG, (poss SH)	L, AL, W, AW	SB, N
Crustacea	Amphipoda	*Hyalella*	*azteca*	CG, (poss SH)	L, AL, W, AW	SB, N
	Branchiopoda	Cladocera	*Bosmina*	CF	L, AL, W, AW	SB, N
		Cladocera	*Daphnia*	CF	L, AL, W, AW	SB, N
	Copepoda		Calanoida	CF (or raptorial)	L, AL, W, AW	SB, N
	Copepoda		Cyclopoida	pred (raptorial)	L, AL, W, AW	SB, N
	Decapoda	Pleocyemata	Astacidae	CG, SHH	W	N
	Isopoda	Asellidae	*Asellus*	CG, (poss. SH)	L, AL, W, AW	SB, N
	Ostracoda			CF	L, AL, W, AW	SB, N

Non-Insect Taxa (Table 1) 3 of 3				FFG	Substrate Days 2-60	Site SB and N
Nematoda				CG	L, AL, W, AW	N
Annelida		Oligochaeta		CG	L, AL, W, AW	SB, N
Platyhelminthes	Turbellaria	Tricladida	Planariidae	pred, CG	W	N
Cnidaria	Hydrozoa	Anthomedusae	*Hydra*	pred	L, AL, W, AW	SB, N
Vertebrata	Minnow (fry)			attached egg sac	L, AL	N

[1] FFG = Functional Feeding Group from Merritt and Cummins (1996): collector-filterer (CF), collector-gatherer (CG), scraper (scr), shredder-herbivore (SHH), may function as shredders (poss SH), predator (pred), piercer (P), piercer-herbivore (PH).

[2] Identified using keys of Merritt and Cummins (1996), Kansas Biological Survey (1985), Schuster and Etnier (1978).

**Simulium meridionale* dominated the simuliids (Pruess, personal communication).

Table 2. Chironomidae of Missouri River sites SB (upstream) and N (downstream) from leaf packs (L), artificial leaves (AL), wood (W), and artificial wood (AW).

Subfamily and Tribe	[2] Taxa Genus and species	[1] FFG	Substrate days 2-60	Site SB and N
Orthocladiinae				
Corynoneurini	*Corynoneura taris*	CG	L, AL, W	N
	Corynoneura sp. 2	CG	W	N
	Thienemanniella xena	CG	L, W, AW	SB, N
Orthocladiini				N
& Metriocnemini	*Cardiocladius* sp.	pred	L	N
	Chaetocladius sp.	CG	AL	N
	* *Cricotopus*	SHH, CG		
	* *bicinctus*		L, AL, W, AW	SB, N
	sylvestris		L, AL, W, AW	SB
	* *tremulus* group		L, AL, W, AW	SB, N
	trifascia group		L, AL, W, AW	SB
	Diplocladius sp.	CG?	AL, W, AW	N
	Eukiefferiella bavarica group	CG, scr, pred	W	N
	Eukiefferiella claripennus group	CG, scr, pred	W	N
	Hydrobaenus sp. 1	scr, CG	L, W, AW	SB
	Hydrobaenus sp. 2	scr, CG	AL, AW	N
	Limnophyes sp.?	CG?	L, AL, W, AW	N
	Nanocladius crassicornus	CG	L, AL, W, AW	SB, N
	Orthocladius obumbratus	CG	L, AL, W, AW	SB, N
	Parakiefferiella sp.?	CG	W, AW	SB
	Parametriocnemus lundbecki	CG	AL	N
	Paraphaenocladius sp.	CG	L, AL, W, AW	SB, N
	Rheocricotopus sp. 1 (*robaki?*)	CG, SHH, pred	AL, W, AW	N
	Rheocricotopus sp. 2	CG, SHH, pred	L, AL, W	N
	Rheosmittia sp.	?	L, W	N

Chironomidae (Table 2)
2 of 3

Subfamily and Tribe	[2] Taxa Genus and species	[1] FFG	Substrate days 2-60	Site SB and N
	Smittia sp.	CG	AL, W	N
Chironominae				
Chironomini	*Chironomus decorus*	CG, CF	W, AW	SB
	Crypotochironomus sp.	pred	L, AL, W	SB, N
	Dicrotendipes	CG, CF, (scr?)		
	neomodestus		L, AL, W, AW	SB, N
	nervosus (Type 1)		W, AW	SB, N
	nervosus (Type 2)		AL	N
	Einfeldia sp.	CG	W	SB
	Endochironomus nigricans	SHH, CF, CG	W, AW	N
	Glypotendipes lobiferus	CF	AL, W, AW	SB, N
	Parachironomus abortivus	pred, CG	L, AL, W	SB, N
	Parachironomus sp. 2	pred, CG	W, AW	SB, N
	Paracladopelma sp.	?	AL, W	N
	Paralauterborniella sp.	CG	AL	N
	* *Paratendipes* sp. 1	CG	L, AL, W, AW	N
	* *Paratendipes* sp. 2	CG	AL, AW	N
	Phaenopsectra flavipes	scr, CG, (CF?)	L, AL, W	N
	Polypedilum	SHH, CG, pred		
	sp.1 (Tripodura)		L, W, AW	SB, N
	convictum (Polypedilum)	CF	L, AL, W, AW	SB, N
	fallax group (Polypedilum)		L, W, AW	N
	illinoense (Polypedilum)		AL, W, AW	SB, N
	scalaenum (Tripodura)		L, W	N
Pseudochironomini	*Pseudochironomus* sp.	CG	L, AL, W, AW	SB, N
Tanytarsini	*Cladotanytarsus* (*Lenziella*) sp.	CG, CF	L, W, AW	N
	* *Micropsectra* sp.	CG	L, AL, W, AW	SB, N

Chironomidae (Table 2)
3 of 3

Subfamily and Tribe	[2] Taxa Genus and species	[1] FFG	Substrate days 2-60	Site SB and N
	* *Paratanytarsus* sp.	?	L, AL, W, AW	SB, N
	Rheotanytarsus distinctissmus group	CF	AL, W, AW	N
	Stempellina sp.	CG	L	N
	Tanytarsus guerlus group	CF, CG	W	N
	Tanytarsus sp. 2	CF, CG	L, W, AW	SB, N
Tanypodinae				
Pentaneurini	*Ablabesmyia* sp. 1	pred, CG	AW	N
	Ablabesmyia sp. 2	pred, CG	AL	N
	Larsia sp.	pred	L, W, AW	N
	**Thienemannimyia* group	pred	L, AL, W, AW	SB, N
Procladiini	*Procladius sublettei*	pred, CG	L	N
Prodiamesinae	*Odontomesa* sp.	CG?	L, AL	N

[1] FFG = Functional Feeding Group from Merritt and Cummins (1996)
CF = collector-filterer and suspension feeder
CG = collector-gatherer and deposit feeder
scr = scraper
SHH = shredder-herbivore
pred = predator

[2] Identified using keys of Merritt and Cummins (1996), Simpson and Bode (1980), Simpson, Bode, and Albu (1982), Stewart and Loch (1973), and Darby (1962).

* = common taxa

Table 1. Lengths of various taxa (mm) collected from substrates at sites SB (upstream) and N (downstream).

Taxa	Length (mm)	*Size class	SB substrates Days 2-60	N substrates Days 2-30
Trichoptera	0.7-18.5	Small-large	****	****
Plecoptera	0.5-12.5	Small-large	****	****
Ephemeroptera	0.5-9.0	Small-large	W, AW	****
Simuliidae	0.5-8.0	Small-large	W, AW, AL	****
Amphipoda	up to 6.5	Small-large	W, AW	****
Isopoda	1.0-7.5	Small-large	W, AW, AL	****
Oligochaeta	up to 35+	Small-large	****	****
Uncommon Taxa:				
Other Diptera				
Ceratopogonidae	8.2	Large	AL	W, AW, AL
Tipulidae	8.0	Large		AW, AL
Culicidae	4.5	Small		AL
Empididae	3.0	Small	W, AW	****
Coleoptera				
Gyrinidae	11.0	Large	W	
Elmidae	4.0-5.0	Small		W, AW, AL
other	1.0-4.0	Small	L, W	AW
Hemiptera (Corixidae)	6.0	Small/large	W	AW
Odonata (Coenagrionidae)	9.0	Large		W
Pulmonata (Physidae)	7.0	Large	AL	****
Decapoda	9.0	Large		W
Large Nematoda	up to 13.0	Small-large		W
Vertebrata (minnow/fry)	6.0-6.8	Small-large		L, AL

*Size class -- Dobson et al. 1995, divided detrivores into large bodied (> 6mm in length) and small bodied (< 6 mm in length) groups. This table includes non-detrivores also.

**** = all substrate types

Table 4. Invertebrate Colonization Summary

a) Invertebrate abundance on substrates from sites SB (upstream) & N (downstream) on days 2-60 (d2-60)

Significant Effects ($p < 0.05$)	**Cottonwood (W)**	**Artificial Wood (AW)**	**Cottonwood leaf pack (L)**	**Artificial leaf pack (AL)**
Substrate effects	Wood treatments		Leaf treatments	
Wood vs. Leaf	W > L	AW > AL	L > W	AL > AW
Site SB	d2-*Ho* d30-Tri[Hyd(*Ho*)]	d7-Inv, chi, Hyd d30-chi,Tri[Hyd(*Ho*),Pol(*N*)], oligo, non-insect	d30-zoo, Collembola	
Site N	d2- Eph(*B*,H) // d7-Inv,Pol,Eph(*C*),oth-Dip	d2-oligo, *Caenis*		d7-zoo, non-insect
Organic vs. Inorganic	W > AW	AW > W	L > AL	AL > L
	N d7-Inv, chi	SB d30-chi, *Hydra* // N d2-oligo	SB d30-oligo	N d7-Tri(Pol), zoo, non-insect
Time effects				
day 0-2 increase	N-Inv, Tri[Hyd(*Ho*),Pol(*N*), Eph(*B*,H), oth Dip, zoo // SB-Tri[Hyd(*Ho*)	N-Inv, chi, Pol(*N*), *Caenis*, oligo, zoo, non-insect	SB-Inv, chi // N-Inv, chi, *Pf*, Eph(*B*)	SB-Hyd(*Ho*)
day 2-7 increase	SB-Plec, Tri[Hyd(*Ho*),Pol(*N*)] N-Inv, Eph(*C*), oligo, Amph	SB-Inv, chi, Tri[Hyd(*Pf*)], oligo, non-insect N-Plec, non-insect	SB-Inv, chi,Tri[Hyd(*Ho*),Pol(*N*)]	SB-zoo // N-Inv, chi, *Necto*, oligo, Isopoda, non-insect
day 2-7 decrease	N-*Ho*			
day 7-30 increase		SB-non-insect, Isopoda, *Hydra*	SB-Inv, zoo, Collembola	ALSB-zoo
day 7-30 decrease	SB-Plec, Pol(*N*)	SB-chi, Tri[Hyd(*Pf*)], non-insect N-Inv, Plec, Eph (*B,C*,H), zoo, oligo, Amph	SB-chi, Tri[Hydr(*Ho*)]	SB-Tri // N-Inv, chi, *Necto*, Pol(*N*), zoo, oligo, Acariformes, non-insect
* day 2-30 increase		SB-*Neureclipsis*	SB-oligo	SB-Inv
* day 2-30 decrease	N-Hyd	N-Pol(*N*)	N-Eph(*B*)	SB-Hyd(*Ho*)
day 30-60 increase	SB-chi, oligo	SB-other Diptera (Simuliidae)		SB-chi, other Diptera (Simuliidae), Tri[Hyd(*Ho*)], *Hydroptila*, oligo
day 30-60 decrease	SB-Pol(*N*)			SB-zoo
*other	d2-60 increase: WSB-Inv			SB7-60 decrease-*Hydroptila*
Site effects				
SB > N	d7-Pol(*N*) d30-chi, Hyd(*Ho*), *Neureclipsis*	d7-Inv, chi, Tri[Hyd(*Ho, Pf*)] // d30-Inv, chi, Tri[Hyd(*Ho,Pf*),Pol(*N*)], oligo, Isopoda, *Hydra*	d7-Inv, chi, Tri[Hyd(*Ho*),Pol(*N*) d30-Inv, chi, Collembola, zoo	d30-Inv, zoo
N > SB	d2-oth-Dip, Eph(*B*,H), oligo d7-oth-Dip, Necto, Eph(*C,B*,H)	d2-*Caenis*, oligo, non-insect d7-Eph(*C,B*,H), Amph	d2-Eph(*B*) d7-non-insect	d7-Necto, Isopoda, Acariforrmes

- All taxa listed are significant at that level: Inv = total invertebrates, chi = chironomids, oth-Dip = other Diptera (excludes chi), Tri[Hyd(*Ho,Pf*),Pol(*N*) = Trichoptera [Hydropsychidae (*H. orris*, *P. flava*), Polycentropodidae (*Neureclipsis*)], *Necto* = *Nectopsyche*, Eph(*B,C*,H) = Ephemeroptera (*Baetis*, *Caenis*, Heptageniidae), Plec = Plecoptera, oligo = Oligochaeta, zoo = zooplankton, "non-insect" = other non-insects (excludes zoo & oligo; included here when not-significant at lower taxonomic levels), Amph = Amphipoda = *Hyallela azteca*

Table 4 (Colonization Summary) Cont.

b) Relative abundance (% of total invertebrate community; days 2-30 combined)

Trt	Chironomidae				Oligochaeta				Zooplankton				Chiron/Oligo/Zoo combined				Trichoptera			
	W	AW	L	AL	W	AW	L	AL	W	AW	L	AL	W	AW	L	AL	W	AW	L	AL
Site SB	57%	55%	23%	23%	14%	9%	3%	4%	22%	27%	68%	69%	93%	91%	95%	96%	6%	7%	5%	5%
Site N	17%	24%	26%	18%	12%	18%	26%	14%	16%	16%	20%	35%	45%	58%	72%	67%	13%	13%	11%	7%

c) Chironomidae and Trichoptera species richness for days 2-30 (no. of individual species)

Trt	W	AW	L	AL
Chironomidae				
Site SB	14	13	14	10
Site N	37	24	26	28
Trichoptera				
Site SB	7	6	5	5
Site N	8	6	5	6

d) Dominant Chironomidae species
(% of chironomid community; derived from combined replicates, per substrate type and date)

Trt	W	AW	L	AL
SB days 2-60				
Orthocladiini/Metriocnemi (94-100%)				
Cricotopus bicinctus	70-88%	81-89%	80-92%	68-91%
Cricotopus tremulus	3-21%	4-10%	3-14%	0-18%
N days 2&7				
Chironominae (52-76%)				
Paratanytarsus (Tanytarsini)	33%, 25%	38%, 17%	30%, 10%	38%, 9%
Micropsectra (Tanytarsini)	9%, 16%	14%, 38%	11%, 23%	13%, 22%
Thienemannimyia (Tanypodinae)	5%, 10%	10%, 3%	7%, 7%	13%, 6%
* N day 30				
Chironominae	83%	100%	100%	94%
Paratendipes spp. (Chironomini)	2%	95%	100%	94%

* Site N, day 30 results coincide with substrate burial

Table 5. ANOVA for effects of substrate, time and site on invertebrate colonization. Since three replicates were not available for SB on day 60, the mean of two replicates for wood (W), artificial wood (AW), and artificial leaf (AL) was added as a third replicate to compare the effects of time; leaf (L) on day 60 was not compared since only one replicate was available.

a. Total number of invertebrates

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Tl Invertebrates	SB	7	AW > AL	0.01	SB	L	d2 > d0	0.01	7	L, AW	SB > N	0.03, 0.00
						L, AW	d7 > d2	0.01, 0.01	30	L, AL, AW	SB > N	0.01, 0.02, 0.01
						L	d30 > d7	0.03				
						AL	d30 > d2	0.02				
						AL, W	d60 > d2	0.01, 0.03				
	N	7	W > AW	0.02	N	W, AW, L	d2 > d0	0.00, 0.00, 0.05				
		7	W > L	0.04		AL, W	d7 > d2	0.04, 0.05				
						AL, AW	d7 > d30	0.01, 0.00				
						AW	d2 > d30	0.01				

b. The most abundant taxa

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Chironomidae	SB	7	AW > AL	0.02	SB	L	d2 > d0	0.04	7	L, AW	SB > N	0.01, 0.00
		30	AW > W	0.00		L, AW	d7 > d2	0.01, 0.01	30	L, W, AW	SB > N	0.03, 0.01, 0.00
		30	AW > AL	0.00		L, AW	d7 > d30	0.03, 0.03				
						AL, W	d60 > d30	0.00, 0.04				
	N	7	W > AW	0.04	N	L, AW	d2 > d0	0.04, 0.02				
						AL	d7 > d2	0.02				
						AL	d7 > d30	0.02				
Oligochaeta	SB	30	L > AL	0.05	SB	AW	d7 > d2	0.03	2	W, AW	N > SB	0.04, 0.00
		30	AW > AL	0.00		L	d30 > d2	0.03	30	AW	SB > N	0.00
						AL, W	d60 > d30	0.04, 0.03				
	N	2	AW > W	0.02	N	AW	d2 > d0	0.00				
		2	AW > AL	0.03		AL, W	d7 > d2	0.02, 0.03				
						AL, AW	d7 > d30	0.01, 0.01				

Table 5b Cont. (2 of 6)

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Zooplankton	SB	30	L > W	0.00	SB	AL	d7 > d2	0.04	30	L, AL	SB > N	0.02, 0.02
						L, AL	*d30 > d7	0.02, 0.02				
						AL	d30 > d60	0.02				
	N	7	*AL > AW	0.03	N	W, AW	d2 > d0	0.05, 0.01				
		7	*AL > L	0.05		AL, AW	*d7 > d30	0.03, 0.00				

* Substrate effects on zooplankton, at site N day 7, coincide with a significant increase in Cyclopoida (p = 0.03 and 0.05, respectively).

* Effects of time on zooplankton from days 0-2 at site N on AW, coincides with a significant increase in Cyclopoida (0.01). Effects of time on zooplankton from days 7-30: 1) at site SB on L, coincide with a signifcant increase in Cyclopoida and Calanoida (p = 0.01 and 0.04, respectively), 2) at site SB on AL, coincide with a significant increase in Cyclopoida (0.02), Calanoida (0.04), Daphnia (0.03), and Bosmina (0.02), and 3) at site N on AL and AW, coincide with a significant increase in Cyclopoida (0.02 and 0.00, respectively).

c. Trichoptera abundance

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Trichoptera	SB	30	W > L	0.03	SB	AL, W	d2 > d0	0.00, 0.00	7	L, AW	SB > N	0.00, 0.02
		30	AW > AL	0.00		L, W, AW	d7 > d2	0.01, 0.04, 0.04	30	AW	SB > N	0.00
	N	7	AL > L	0.04		L, AL, AW	d7 > d30	0.01, 0.05, 0.04				
						AL	d60 > d30	0.00				
					N	W	d2 > d0	0.03				
Hydropsychidae	SB	7	AW >AL	0.05	SB	AL, W	d2 > d0	0.00, 0.00	7	L, AW	SB > N	0.00, 0.01
		30	AW > AL	0.00		L, W, AW	d7 > d2	0.01, 0.05, 0.02	30	W, AW	SB > N	0.03, 0.00
		30	W > L	0.02		L, AW	d7 > d30	0.01, 0.02				
						AL	d2 > d30	0.01				
						AL	d60 >d30	0.04				
					N	W	d2 > d0	0.02				
						W	d2 > d30	0.03				

H. orris Cont. (Table 5c) 3 of 6

	Substrate effects				Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
H. orris	SB	2	W > L	0.00	SB	AL, W	d2 > d0	0.03, 0.00	7	L, AW	SB > N	0.01, 0.01
		30	W > L	0.00		L, W	d7 > d2	0.01, 0.05	30	W, AW	SB > N	0.04, 0.00
		30	AW > AL	0.00		L	d7 > d30	0.01				
						AL	d2 > d30	0.03				
						AL	d60 >d30	0.05				
					N	W	d2 > d0	0.01				
						W	d2 > d7	0.03				
P. flava					SB	AW	d7 > d2, 30	0.02, 0.02	7	AW	SB > N	0.01
					N	L	d2 > d0	0.02	30	AW	SB > N	0.00
Polycentropodid	SB	30	AW > AL	0.00	SB	L, W	d7 > d2	0.01, 0.01	7	L, W	SB > N	0.00, 0.04
						W	d7 > d30	0.03	30	AW	SB > N	0.00
						W	d30 > d60	0.02				
	N	7	AL > L	0.02	N	W, AW	d2 > d0	0.04, 0.03				
		7	W > L	0.04		AL	d7 > d30	0.02				
						AW	d2 > d30	0.03				
Neureclipsis	SB	30	AW > AL	0.00	SB	L, W	d7 > d2	0.01, 0.01	7	L, W	SB > N	0.00, 0.00
						W	d7 > d30	0.03	30	W, AW	SB > N	0.00, 0.00
						W	d30 > d60	0.02				
						AW	d30 > d2	0.05				
					N	W, AW	d2 > d0	0.04, 0.03				
						AL	d7 > d30	0.02				
						AW	d2 > d30	0.03				
Other Trich					SB	AL	d7 > d60	0.00	7	AL	N > SB	0.02
						AL	d60 > d30	0.00				
					N	AL	d7 > d2	0.03				
						AL, AW	d7 > d30	0.01, 0.04				

Other Trich (Table 5e Cont.) 4 of 6

	Substrate effects				Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Hydroptilidae (*Hydroptila*)					SB	AL	d7 > d60	0.00				
							d60 > d30	0.00				
Nectopsyche					N	AL	d7 > d2,30	0.03, 0.01	7	AL, W	N > SB	0.01, 0.01

d. Ephemeroptera abundance

	Substrate effects				Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Ephemeroptera	N	2	W > L	0.00	N	L, W	d2 > d0	0.02, 0.00	2	L, W	N > SB	0.02, 0.00
		7	W > L	0.01		L	d2 > d30	0.02	7	W, AW	N > SB	0.00, 0.00
						W	d7 > d2	0.03				
						AW	d7 > d30	No variance				
Baetidae (*Baetis*)	N	2	W > L	0.03	N	L, W	d2 > d0	0.01, 0.01	2	L, W	N > SB	0.01, 0.01
						L	d2 > d30	0.01	7	W, AW	N > SB	0.02, 0.02
						AW	d7 > d30	0.02				
Caenidae (*Caenis*)	N	2	AW > AL	0.02	N	AW	d2 > d0	0.02	2	AW	N > SB	0.02
		7	W > L	0.02		W	d7 > d2	0.03	7	W, AW	N > SB	0.01, 0.02
						AW	d7 > d30	0.02				
Heptageniidae (*Stenonema*)	N	2	W > L	0.02	N	W	d2 > d0	0.02	2	W	N > SB	0.02
						AW	d7 > d30	0.00	7	W, AW	N > SB	0.04, 0.00

e. Other insect taxa (excludes chironomids) (Table 5 Cont.; 5 of 6)

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Tl other Insecta	SB	30	AW > AL	0.00	SB	W, AL	d2 > d0	0.00, 0.01	2	W	N > SB	0.00
						L, W, AW	d7 > d2	0.01, 0.03, 0.03	7	L	SB > N	0.04
						AW	d7 > d30	0.05	30	AW	SB > N	0.00
						AL	d60 > d30	0.00				
						W	d30 > d2	0.01				
	N	2	W > L	0.04	N	W	d2 > d0	0.00				
		7	W > L	0.00		AW	d7 > d30	0.00				
		7	W > AW	0.01								
other Diptera	N	7	W > L	0.02	SB	*AL	d60 > d7,30	0.01, 0.01	2	W	N > SB	0.04
						*AW	d60 > d2,7,30	0.00, 0.00, 0.00	7	W	N > SB	0.01
					N	W	d2 > d0	0.04				
Plecoptera					SB	W	d7 > d2,30,60	0.03, 0.03, 0.03				
					N	AW	d7 > d2,30	0.02, 0.00				
Collembola	SB	30	L > W	0.05	SB	L	d30 > d2,7	0.01, 0.01	30	L	SB > N	0.01

* Effects of time on total other diptera abundance at SB, coincide with significant increases in Simuliidae abundance by day 60 for AL (0.01) and AW (0.00).

f. Other non-insect taxa; excludes oligochaetes and zooplankton

Substrate effects					Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
other non-Insecta	SB	30	AW > AL	0.03	SB	AW	d30 > d2,7	0.02, 0.03	2	AW	N > SB	0.05
	N	7	AL > L	0.00	N	AW	d2 > d0	0.01	7	L, AL, AW	N > SB	0.03, 0.00, 0.02
		7	AL > AW	0.01		AL	d7 > d2,30	0.00, 0.00	30	AW	SB > N	0.04
						AW	d7 > d2	0.02				
Amphipoda (*H. azteca*)					N	W	d7 > d2	0.04	7	AW	N > SB	0.00
						AW	d7 > d30	0.01				
Isopoda					SB	AW	d30 > d2,7	0.02	7	AL	N > SB	0.03

Other non-insect taxa (Table 5f Cont.) 6 of 6												
	Substrate effects				Effects of time (d)				Site effects			
taxa	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
(*Asellus*)					N	AL	d7 > d2	0.03	30	AW	SB > N	0.02
Hydra	SB	30	AW > W	0.02	SB	AW	d30 > d2,7	0.00, 0.03	30	AW	SB > N	0.01
		30	AW > AL	0.01								
Acariformes					N	AL	d7 > d30	0.03	7	AL	N > SB	0.03

The following tables, Table 6 (total invertebrates) and Table 7 (Chironomidae), contain abundance and relative abundance (% of community) data collected from wood (W), artificial wood (AW), leaf (L), and artificial leaf (AL) treatments, at sites SB (upstream) and N (downstream), on days (D) 2, 7, 30, and 60. Functional Feeding Group (FFG) of taxa as described by Merritt and Cummins (1996) are also included: collector–gatherer (CG), collector-filterer (CF), shredder–herbivore (SHH), shredder-detrivore (SHD), scraper (Scr), piercer–herbivore (PH), and predator (Pred). Taxa not listed as shredders but whose feeding may lead to size particle reduction are indicated as "(poss. SH)".

Table 6. Total invertebrates (1 of 14)

Taxa WSBD2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	165, 34, 64		263	88(69)		
Chironomidae	134, 18, 48	81, 53, 75	200	67(60)	70(15)	Mainly CG
Total other Insecta	9, 14, 8	5, 41, 12	31	10(3)	20(19)	
Coleoptera (*Peltodytes*) adult	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	P,SHH,Pred
Trichoptera	9, 13, 8	5, 38, 12	30	10(3)	19(17)	
Hydropsychidae	7, 6, 7	4, 18, 11	20	7(1)	11(7)	CF
H. orris	7, 5, 6	4, 15, 9	18	6(1)	9(5)	
P. flava	0, 1, 1	0, 3, 2	2	1(1)	1(1)	
Polycent (*Neureclipsis*)	2, 6, 1	1, 18, 2	9	3(3)	7(9)	CF,SHH,Pred
Other Trich (*Nectopsyche*)	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	SHH,CG
Other (Acariformes)	1, 0, 0	1, 0, 0	1	<1(1)	<1(<1)	Pred
Oligochaeta	0, 0, 1	0, 0, 2	1	<1(1)	<1(1)	CG
Zooplankton (Copepoda)	21, 2, 7	13, 6, 11	30	10(10)	10(4)	
Calanoida	10, 2, 5	6, 6, 8	17	6(4)	7(1)	CF
Cyclopoida	11, 0, 2	7, 0, 3	13	4(6)	3(3)	Pred

Taxa WSBD7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	447, 1436, 360		2243	748(598)		
Chironomidae	335, 1014, 253	75, 71, 70	1602	534(418)	72(3)	Mainly CG
Total other Insecta	34, 71, 39	8, 5, 11	144	48(20)	8(3)	
Coleoptera	1, 1, 0	<1, <1, 0	2	1(1)	<1(<1)	
Haliplid (*Peltodytes*) adult	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	P,SHH,Pred
Hydrophilidae (larvae)	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	Pred
Other Diptera (unknown)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	
Plecoptera (*Isoperla*)	1, 3, 2	<1, <1, 1	6	2(1)	<1(<1)	Pred,CG
Trichoptera	32, 67, 36	7, 5, 10	135	45(19)	7(3)	
Hydropsychidae	20, 40, 18	4, 3, 5	78	26(12)	4(1)	CF
H. orris	14, 27, 14	3, 2, 4	55	18(7)	3(1)	
H. simulans	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	
P. flava	6, 12, 4	1, 1, 1	22	7(4)	1(<1)	
Polycentropodidae	12, 23, 18	3, 2, 5	53	18(5)	3(2)	CF,SHH,Pred
Neureclipsis	12, 19, 18	3,1,5	49	16(4)	3(2)	
Polycentropus	0, 4, 0	0, <1, 0	4	1(2)	<1(<1)	
Other Trich (*Hydroptila*)	0, 4, 0	0, <1, 0	4	1(2)	<1(<1)	PH,Scr
Other	0, 17, 2	0, 1, 1	19	6(9)	1(1)	
Amphipoda (*H. azteca*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG(poss. SH)
Hydra	0, 17, 1	0, 1, <1	18	6(9)	<1(1)	Pred
Oligochaeta	65, 311, 48	14, 22, 13	424	141(147)	16(4)	CG
Zooplankton	13, 23, 18	3, 2, 5	54	18(5)	3(2)	
Cladocera (*Daphnia*)	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	CF
Copepoda	13, 22, 18	3, 1, 5	53	18(4)	3(2)	
Calanoida	9, 13, 10	2, 1, 3	32	11(2)	2(1)	CF
Cyclopoida	4, 9, 8	1, 1, 2	21	7(3)	1(1)	Pred

Table 6 (2 of 14)

Taxa WSBD30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	216, 604, 207		1027	342(227)		
Chironomidae	84, 64, 62	39, 11, 30	210	70(12)	26(14)	Mainly CG
Total other Insecta	20, 18, 18	9, 3, 9	56	19(1)	7(3)	
Coleoptera	0, 0, 2	0, 0, 1	2	1(1)	<1(1)	
Gyrinid (*Dineutus*) adult	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	Pred
Unknown	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	
Collembola	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG
Other Diptera	3, 1, 1	1, <1, <1	5	2(1)	1(1)	
Empididae (*Hemerodromia*)	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	Pred,CG
Unknown	3, 0, 1	1, 0, <1	4	1(1)	1(1)	
Hemiptera (Corixidae)	0, 2, 0	0, <1, 0	2	1(1)	<1(<1)	PH,Pred,Scr
Trichoptera	17, 15, 14	8, 2, 7	46	15(1)	6(3)	
Hydropsychidae	10, 10, 6	5, 2, 3	26	9(2)	3(1)	CF
H. orris	7, 8, 6	3, 1, 3	21	7(1)	2(1)	
P. flava	3, 2, 0	1,<1,0	5	2(1)	1(1)	
Polycent (*Neureclipsis*)	7, 5, 7	3, 1, 3	19	6(1)	2(1)	CF,SHH,Pred
Other Trich (*Hydroptila*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	PH,Scr
Other	7, 0, 0	3, 0, 0	7	2(4)	1(2)	
Amphipoda (*H.azteca*)	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	CG (poss SH)
Hydra	2, 0, 0	1, 0, 0	2	1(1)	<1(<1)	Pred
Isopoda (*Asellus*)	4, 0, 0	2, 0, 0	4	1(2)	1(1)	CG (poss SH)
Oligochaeta	44, 7, 7	20, 1, 3	58	19(21)	8(10)	CG
Zooplankton	61, 515, 120	28, 85, 58	696	232(247)	57(28)	
Cladocera	25, 100, 30	12, 17, 14	155	52(42)	14(2)	
Bosmina	1, 2, 1	<1, <1, <1	4	1(1)	<1(<1)	CF
Daphnia	24, 98, 29	11, 16, 14	151	50(41)	14(3)	CF
Copepoda	36, 415, 90	17, 69, 43	541	180(205)	43(26)	
Calanoida	5, 95, 30	2, 16, 14	130	43(46)	11(7)	CF
Cyclopoida	31, 320, 60	14, 53, 29	411	137(159)	32(19)	Pred

Taxa WSBD60	N (r = 2)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	348, 835		1183	591(344)		
Chironomidae	192, 532	55, 64	724	362(240)	59(6)	Mainly CG
Total other Insecta	23, 226	7, 27	249	124(143)	17(14)	
Other Diptera	1, 15	<1, 2	16	8(10)	1(1)	
Simulid (*Simulium*)	1, 14	<1, 2	15	7(9)	1(1)	CF
Unknown	0, 1	0, <1	1	<1(1)	<1(<1)	
Ephemeroptera (*Stenonema*)	1, 2	<1, <1	3	1(1)	<1(<1)	Scr,CG
Trichoptera	21, 209	6, 25	230	115(133)	15(13)	
Hydropsychidae	17, 192	5, 23	209	104(124)	14(13)	CF
H. orris	16, 190	5, 23	206	103(123)	14(13)	
P. flava	1, 2	<1, <1	3	1(1)	<1(<1)	
Polycent (*Neureclipsis*)	4, 1	1, <1	5	2(2)	1(1)	CF,SHH,Pred
Other Trich (*Hydroptila*)	0, 16	0, 2	16	8(11)	1(1)	PH,Scr
Other	30, 1	9, <1	31	15(20)	4(6)	
Hydra	28, 1	8, <1	29	14(19)	4(6)	Pred
Isopoda (*Asellus*)	2, 0	1, 0	2	1(1)	<1(<1)	CG (poss SH)
Oligochaeta	83, 54	24, 6	137	68(20)	15(12)	CG
Zooplankton	20, 22	6, 3	42	21(1)	4(2)	
Cladocera (*Daphnia*)	3, 5	1, 1	8	4(1)	1(<1)	CF
Copepoda	17, 17	5, 2	34	17(0)	3(2)	
Calanoida	10, 8	3, 1	18	9(1)	2(1)	CF
Cyclopoida	7, 9	2, 1	16	8(1)	1(1)	Pred

Table 6 (3 of 14)

Taxa AWSBD2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	157, 18, 101		276	92(70)		
Chironomidae	86, 11, 82	55, 61, 81	179	60(42)	66(14)	Mainly CG
Total other Insecta (Trichop)	15, 1, 12	10, 6, 12	28	9(7)	9(3)	
Hydropsychidae	9, 0, 8	6, 0, 8	17	6(5)	5(4)	CF
H. orris	7, 0, 4	5, 0, 4	11	4(3)	3(2)	
P. flava	2, 0, 4	1, 0, 4	6	2(2)	2(2)	
Polycentropodidae	6, 1, 3	4, 6, 3	10	3(2)	4(1)	CF,SHH,Pred
Neureclipsis	5, 1, 3	3, 6, 3	9	3(2)	4(1)	
Polycentropus	1, 0, 0	1, 0, 0	1	<1(1)	<1(<1)	
Other Trich (*Nectopsyche*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	SHH,CG
Other (Amphipod – *H. azteca*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CG (poss SH)
Zooplankton (Copepoda)	56, 6, 6	36, 33, 6	68	23(29)	25(16)	
Calanoida	25, 4, 3	16, 22, 3	32	11(12)	14(10)	CF
Cyclopoida	31, 2, 3	20, 11, 3	36	12(16)	11(8)	Pred

Taxa AWSBD7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	447, 390, 591		1428	476(104)		
Chironomidae	295, 291, 462	66, 75, 78	1048	349(98)	73(6)	Mainly CG
Total other Insecta	28, 48, 66	6, 12, 11	142	47(19)	10(3)	
Ephemeroptera (*Stenonema*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	Scr,CG
Plecoptera (*Isoperla*)	1, 2, 0	<1, <1, 0	3	1(1)	<1(<1)	Pred,CG
Trichoptera	27, 46, 65	6, 12, 11	138	46(19)	10(3)	
Hydropsychidae	17, 32, 34	4, 8, 6	83	28(9)	6(2)	CF
H. orris	8, 19, 14	2, 5, 2	41	14(5)	3(2)	
P. flava	9, 13, 20	2, 3, 3	42	14(6)	3(1)	
Polycentropodidae	8, 14, 29	2, 4, 5	51	17(11)	3(2)	CF, SHH, Pred
Neureclipsis	8, 10, 25	2, 3, 4	43	14(9)	3(1)	
Polycentropus	0, 4, 4	0, 1, 1	8	3(2)	1(<1)	
Other Trichoptera	2, 0, 2	<1, 0, <1	4	1(1)	<1(<1)	
Hydroptila	1, 0, 1	<1, 0, <1	2	1(1)	<1(<1)	PH,Scr
Nectopsyche	1, 0, 1	<1, 0, <1	2	1(1)	<1(<1)	SHH,CG
Other (*Hydra*)	2, 1, 0	<1, <1, 0	3	1(1)	<1(<1)	Pred
Oligochaeta	87, 32, 43	19, 8, 7	162	54(29)	12(7)	CG
Zooplankton	35, 18, 20	8, 5, 3	73	24(9)	5(2)	
Cladocera	0, 3, 2	0, 1, <1	5	2(1)	<1(<1)	
Bosmina	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	CF
Daphnia	0, 2, 2	0, <1, <1	4	1(1)	<1(<1)	CF
Copepoda	35, 15, 18	8, 4, 3	68	23(11)	5(3)	
Calanoida	14, 11, 10	3, 3, 2	35	12(2)	3(1)	CF
Cyclopoida	21, 4, 8	5, 1, 1	33	11(9)	2(2)	Pred

Table 6 (4 of 14)

Taxa AWSBD30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	628, 367, 350		1345	448(156)		
Chironomidae	145, 171, 148	23, 47, 42	464	155(14)	37(12)	Mainly CG
Total other Insecta	19, 14, 15	3, 4, 4	48	16(3)	4(1)	
Collembola	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	CG
Other Diptera (*Hemerodromia*)	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred,CG
Ephemeroptera (*Caenis*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG,Scr
Plecoptera (*Isoperla*)	1, 0, 1	<1, 0, <1	2	1(1)	<1(<1)	Pred,CG
Trichoptera	16, 14, 13	3, 4, 4	43	14(1)	3(1)	
Hydropsychidae	7, 6, 6	1, 2, 2	19	6(1)	1(<1)	CF
H. orris	7, 6, 4	1, 2, 1	17	6(1)	1(<1)	
P. flava	0, 0, 2	0, 0, 1	2	1(1)	<1(<1)	
Polycentropodidae	7, 6, 7	1, 2, 2	20	7(1)	2(<1)	CF,SHH,Pred
Neureclipsis	6, 6, 7	1, 2, 2	19	6(1)	1(<1)	
Polycentropus	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	
Other Trich (*Hydroptila*)	2, 2, 0	<1, <1, 0	4	1(1)	<1(<1)	PH,Scr
Other	9, 13, 5	1, 3, 1	27	9(4)	2(1)	
Amphipoda (*H. azteca*)	1, 3, 0	<1, 1, 0	4	1(1)	<1(<1)	CG (poss SH)
Hydra	6, 9, 4	1, 2, 1	19	6(2)	1(1)	Pred
Isopoda (*Asellus*)	2, 1, 1	<1, <1, <1	4	1(1)	<1(<1)	CG (poss SH)
Oligochaeta	37, 32, 46	6, 9, 13	115	38(7)	9(4)	CG
Zooplankton	418, 137, 136	67, 37, 39	691	230(162)	48(16)	
Cladocera	68, 30, 37	11, 8, 11	135	45(20)	10(1)	
Bosmina	1, 0, 1	<1, 0, <1	2	1(1)	<1(<1)	CF
Daphnia	67, 30, 36	11, 8, 10	133	44(20)	10(1)	CF
Copepoda	350, 107, 99	56, 29, 28	556	185(143)	38(16)	
Calanoida	84, 33, 25	13, 9, 7	142	47(32)	10(3)	CF
Cyclopoida	266, 74, 74	42, 20, 21	414	138(111)	28(12)	Pred

Taxa AWSBD60	N (r = 2)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	1039, 212		1251	625(585)		
Chironomidae	573, 165	55, 78	738	369(288)	66(16)	Mainly CG
Total other Insecta	126, 10	12, 5	136	68(82)	8(5)	
Other Diptera (*Simulium*)	3, 3	<1, 1	6	3(0)	1(1)	CF
Plecoptera (*Isoperla*)	1, 0	<1, 0	1	<1(1)	<1(<1)	Pred,CG
Trichoptera	122, 7	12, 3	129	64(81)	7(6)	
Hydropsychidae	105, 6	10, 3	111	55(70)	6(5)	CF
Cheumatopsyche	1, 0	<1, 0	1	<1(1)	<1(<1)	
H. bidens	1, 0	<1, 0	1	<1(1)	<1(<1)	
H. orris	93, 5	9, 2	98	49(62)	6(5)	
P. flava	10, 1	1, <1	11	5(6)	1(<1)	
Polycent (*Neureclipsis*)	15, 1	1, <1	16	8(10)	1(1)	CF,SHH,Pred
Other Trich (*Hydroptila*)	2, 0	<1, 0	2	1(1)	<1(<1)	PH,Scr
Other	44, 0	4, 0	44	22(31)	2(3)	
Hydra	41, 0	4, 0	41	20(29)	2(3)	Pred
Isopoda (*Asellus*)	3, 0	<1, 0	3	1(2)	<1(<1)	CG (poss SH)
Oligochaeta	225, 24	22, 11	249	124(142)	16(7)	CG
Zooplankton	72, 12	7, 6	84	42(42)	6(1)	
Cladocera (*Daphnia*)	9, 6	1, 3	15	7(2)	2(1)	CF
Copepoda	63, 6	6, 3	69	34(40)	4(2)	
Calanoida	48, 4	5, 2	52	26(31)	3(2)	CF
Cyclopoida	15, 2	1, 1	17	8(9)	1(<1)	Pred

Table 6 (5 of 14)

Taxa LSBD2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	48, 23, 28		99	33(13)		
Chironomidae	35, 19, 11	73, 83, 39	65	22(12)	65(23)	Mainly CG
Total other Insecta	12, 1, 4	25, 4, 14	17	6(6)	14(10)	
Coleoptera	2, 0, 0	4, 0, 0	2	1(1)	1(2)	
Staphylinidae	1, 0, 0	2, 0, 0	1	<1(1)	1(1)	Pred
Unknown	1, 0, 0	2, 0, 0	1	<1(1)	1(1)	
Plecoptera (*Isoperla*)	1, 0, 1	2, 0, 4	2	1(1)	2(2)	Pred,CG
Trichoptera	9, 1, 3	19, 4, 11	13	4(4)	11(7)	
Hydropsychidae	6, 1, 1	12, 4, 4	8	3(3)	7(5)	CF
H. orris	0, 1, 0	0, 4, 0	1	<1(1)	1(2)	
P. flava	6, 0, 1	12, 0, 4	7	2(3)	5(6)	
Polycent (*Neureclipsis*)	3, 0, 2	6, 0, 7	5	2(1)	4(4)	CF,SHH,Pred
Zooplankton (Copepoda)	1, 3, 13	2, 13, 46	17	6(6)	20(23)	
Calanoida	1, 2, 8	2, 9, 29	11	4(4)	13(14)	CF
Cyclopoida	0, 1, 5	0, 4, 18	6	2(3)	7(9)	Pred

Taxa LSBD7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	165, 126, 211		502	167(43)		
Chironomidae	120, 80, 157	73, 63, 74	357	119(38)	70(6)	Mainly CG
Total other Insecta	31, 19, 29	19, 15, 14	79	26(6)	16(3)	
Plecoptera (*Isoperla*)	5, 1, 0	3, 1, 0	6	2(3)	1(2)	Pred,CG
Trichoptera	26, 18, 29	16, 14, 14	73	24(6)	15(1)	
Hydropsychidae	16, 10, 17	10, 8, 8	43	14(4)	9(1)	CF
H. orris	9, 8, 15	5, 6, 7	32	11(4)	6(1)	
H. simulans	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	
P. flava	7, 2, 1	4, 2, <1	10	3(3)	2(2)	
Polycent (*Neureclipsis*)	10, 7, 11	6, 6, 5	28	9(2)	6(<1)	CF,SHH,Pred
Other Trich (*Hydroptila*)	0, 1, 1	0, 1, <1	2	1(1)	<1(<1)	PH,scr
Oligochaeta	5, 19, 7	3, 15, 3	31	10(8)	7(7)	CG
Zooplankton	9, 8, 18	5, 6, 8	35	12(5)	7(2)	
Cladocera (*Daphnia*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CF
Copepoda	9, 8, 17	5, 6, 8	34	11(5)	7(1)	
Calanoida	3, 4, 12	2, 3, 6	19	6(5)	4(2)	CF
Cyclopoida	6, 4, 5	4, 3, 2	15	5(1)	3(1)	Pred

Taxa LSBD30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	454, 310, 609		1373	458(149)		
Chironomidae	37, 54, 17	8, 17, 3	108	36(18)	9(7)	Mainly CG
Total other Insecta	9, 12, 4	2, 4, 1	25	8(4)	2(2)	
Collembola	1, 2, 2	<1, 1, <1	5	2(1)	<1(<1)	CG
Other Diptera (unknown)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	
Trichoptera	8, 10, 1	2, 3, <1	19	6(5)	2(1)	
Hydropsychidae	3, 3, 0	1, 1, 0	6	2(2)	<1(<1)	CF
H. orris	2, 2, 0	<1, 1, 0	4	1(1)	<1(<1)	
P. flava	1, 1, 0	<1, <1, 0	2	1(1)	<1(<1)	
Polycent (*Neureclipsis*)	5, 7, 1	1, 2, <1	13	4(3)	1(1)	CF,SHH,Pred
Other	2, 0, 2	<1, 0, <1)	4	1(1)	<1(<1)	
Acariformes	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	Pred
Hydra	2, 0, 1	<1, 0, <1	3	1(1)	<1(<1)	Pred
Oligochaeta	6, 22, 19	1, 7, 3	47	16(8)	4(3)	CG
Zooplankton	400, 222, 567	88, 72, 93	1189	396(172)	84(11)	
Cladocera	69, 26, 127	15, 8, 21	222	74(51)	15(6)	

LSBD30 (Cont.) Table 6 (6 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Bosmina	10, 2, 14	2, 1, 2	26	9(6)	2(1)	CF
Daphnia	59, 24, 113	13, 8, 19	196	65(45)	13(5)	CF
Copepoda	330, 196, 440	73, 63, 72	966	322(122)	69(5)	
Calanoida	56, 34, 95	12, 11, 16	185	62(31)	13(2)	CF
Cyclopoida	274, 162, 345	60, 52, 57	781	260(92)	56(4)	Pred
Ostracoda	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	CF

Taxa LSBD60	N (r = 1)	N (%)	FF Group
Total Invertebrates	227		
Chironomidae	104	46	Mainly CG
Trichoptera (*Neureclipsis*)	2	1	CF,SHH,Pred
Other (*Hydra*)	2	1	Pred
Oligochaeta	13	6	CG
Zooplankton	106	47	
Cladocera (*Daphnia*)	17	7	CF
Copepoda	89	39	
Calanoida	43	19	CF
Cyclopoida	46	20	Pred

Taxa ALSBD2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	53, 11, 13		77	26(24)		
Chironomidae	38, 3, 6	72, 27, 46	47	16(19)	48(22)	Mainly CG
Total other Insecta	4, 4, 2	8, 36, 15	10	3(1)	20(15)	
Other Diptera (Ceratopogonidae)	0, 1, 0	0, 9, 0	1	<1(1)	3(5)	CG,Pred
Plecoptera (*Isoperla*)	1, 0, 0	2, 0, 0	1	<1(1)	1(1)	Pred,CG
Trichoptera (Hydropsychidae)	3, 3, 2	6, 27, 15	8	3(1)	16(11)	CF
H. orris	2, 3, 1	4, 27, 8	6	2(1)	13(13)	
P. flava	1, 0, 1	2, 0, 8	2	1(1)	3(4)	
Oligochaeta	0, 4, 0	0, 36, 0	4	1(2)	12(21)	CG
Zooplankton	11, 0, 5	21, 0, 38	16	5(5)	20(19)	
Cladocera (*Daphnia*)	0, 0, 1	0, 0, 8	1	<1(1)	3(4)	CF
Copepoda	11, 0, 4	21, 0, 31	15	5(6)	17(16)	
Calanoida	6, 0, 0	11, 0, 0	6	2(3)	4(7)	CF
Cyclopoida	5, 0, 4	9, 0, 31	9	3(3)	13(16)	Pred

Taxa ALSBD7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	235, 61, 116		412	137(89)		
Chironomidae	156, 15, 51	66, 25, 44	222	74(73)	45(21)	Mainly CG
Total other Insecta	29, 25, 6	12, 41, 5	60	20(12)	19(19)	
Plecoptera (*Isoperla*)	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred,CG
Trichoptera	28, 25, 6	12, 41, 5	59	20(12)	19(19)	
Hydropsychidae	17, 0, 3	7, 0, 3	20	7(9)	3(4)	CF
H. orris	8, 0, 3	3, 0, 3	11	4(4)	2(2)	
P. flava	9, 0, 0	4, 0, 0	9	3(5)	1(2)	
Polycentropodidae	10, 25, 3	4, 41, 3	38	13(11)	16(22)	CF,SHH,Pred
Neureclipsis	8, 25, 3	3, 41, 3	36	12(11)	16(22)	
Polycentropus	2, 0, 0	1, 0, 0	2	1(1)	<1(<1)	
Other Trich (*Hydroptila*)	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	PH,Scr
Other	0, 2, 1	0, 3, 1	3	1(1)	1(2)	
Hydra	0, 2, 0	0, 3, 0	2	1(1)	1(2)	Pred
Physidae (*Physa*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(<1)	Scr,CG,(poss SH)
Oligochaeta	13, 5, 22	5, 8, 19	40	13(8)	11(7)	CG

ALSB7 (Cont.) Table 6 (7 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Zooplankton	37, 14, 36	16, 23, 31	87	29(13)	23(8)	
Cladocera (*Daphnia*)	4, 2, 0	2, 3, 0	6	2(2)	2(2)	CF
Copepoda	33, 12, 36	14, 20, 31	81	27(13)	22(9)	
Calanoida	7, 7, 15	3, 11, 13	29	10(5)	9(5)	CF
Cyclopoida	26, 5, 21	11, 8, 18	52	17(11)	12(5)	Pred

Taxa ALSBD30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	384, 150, 267		801	267(117)		
Chironomidae	22, 3, 3	6, 2, 1	28	9(11)	3(2)	Mainly CG
Total other Insecta	0, 2, 1	0, 1, <1	3	1(1)	1(1)	
Collembola	0, 1 ,1	0, 1, <1	2	1(1)	<1(<1)	CG
Trichoptera (*P. flava*)	0, 1, 0	0, 1, 0	1	<1(1)	<1(<1)	CF
Other (Isopoda – *Asellus*)	2, 0, 0	<1, 0, 0	2	1(1)	<1(<1)	CG (poss SH)
Oligochaeta	0, 1, 3	0, 1, 1	4	1(1)	1(1)	CG
Zooplankton	360, 144, 260	94, 96, 97	764	255(108)	96(2)	
Cladocera	62, 24, 37	16, 16, 14	123	41(19)	15(1)	
Bosmina	4, 2, 2	1, 1, 1	8	3(1)	1(<1)	CF
Daphnia	58, 22, 35	15, 15, 13	115	38(18)	14(1)	CF
Copepoda	298, 120, 223	78, 80, 83	641	214(89)	80(3)	
Calanoida	100, 36, 63	26, 24, 24	199	66(32)	25(1)	CF
Cyclopoida	198, 84, 160	52, 56, 60	442	147(58)	56(4)	Pred

Taxa ALSBD60	N (r = 2)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	247, 131		378	189(82)		
Chironomidae	106, 71	43, 54	177	88(25)	49(8)	Mainly CG
Total other Insecta	34, 24	14, 18	58	29(7)	16(3)	
Other Diptera (*Simulium*)	2, 1	1, 1	3	1(1)	1(<1)	CF
Trichoptera	32, 23	13, 18	55	27(6)	15(3)	
Hydropsychidae (H. orris)	28, 8	11, 6	36	18(14)	9(4)	CF
Polycent (Neureclipsis)	0, 12	0, 9	12	6(8)	5(6)	CF,SHH,Pred
Hydroptilidae (Hydroptila)	4, 3	2, 2	7	3(1)	2(<1)	PH,Scr
Other	0, 3	0, 2	3	1(2)	1(2)	
Hydra	0, 2	0, 1	2	1(1)	1(1)	Pred
Isopoda (Asellus)	0, 1	0, 1	1	<1(1)	<1(<1)	CG (poss SH)
Oligochaeta	58, 17	23, 13	75	37(29)	18(7)	CG
Zooplankton	49, 16	20, 12	65	32(23)	16(5)	
Cladocera (Daphnia)	6, 4	2, 3	10	5(1)	3(<1)	CF
Copepoda	43, 12	17, 9	55	27(22)	13(6)	
Calanoida	38, 10	15, 8	48	24(20)	11(5)	CF
Cyclopoida	5, 2	2, 1	7	3(2)	2(<1)	Pred

Taxa WND2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	72, 60, 108		240	80(25)		
Chironomidae	4, 14, 25	6, 23, 23	43	14(10)	17(10)	Mainly CG
Total other Insecta	44, 35, 48	61, 58, 44	127	42(7)	55(9)	
Collembola	1, 0, 0	1, 0, 0	1	<1(1)	<1(1)	CG
Other Diptera	10, 5, 3	14, 8, 3	18	6(4)	8(6)	
Ceratopogonidae	0, 1, 0	0, 2, 0	1	<1(1)	1(1)	CG,Pred
Empidid (*Hemerodromia*)	0, 2, 0	0, 3, 0	2	1(1)	1(2)	Pred,CG
Simuliidae (*Simulium*)	5, 1, 3	7, 2, 3	9	3(2)	4(3)	CF
Unknown	5, 1, 0	7, 2, 0	6	2(3)	3(4)	

WND2 (Cont.) Table 6 (8 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Ephemeroptera	10, 14, 10	14, 23, 9	34	11(2)	15(7)	
Baetidae (*Baetis*)	6, 5, 3	8, 8, 3	14	5(1)	6(3)	CG,Scr
Caenidae (*Caenis*)	2, 2, 0	3, 3, 0	4	1(1)	2(2)	CG,Scr
Heptageniidae (*Stenonema*)	2, 6, 6	3, 10, 6	14	5(2)	6(4)	Scr,CG
Tricoryithidae (*Tricorythodes*)	0, 1, 1	0, 2, 1	2	1(1)	1(1)	CG
Plecoptera (*Isoperla*)	1, 5, 2	1, 8, 2	8	3(2)	4(4)	Pred,CG
Trichoptera	22, 11, 33	31, 18, 31	66	22(11)	26(7)	
Hydropsychidae	18, 10, 26	25, 17, 24	54	18(8)	22(5)	CF
H. orris	17, 10, 24	24, 17, 22	51	17(7)	21(4)	
H. simulans	1, 0, 0	1, 0, 0	1	<1(1)	<1(1)	
P. flava	0, 0, 2	0, 0, 2	2	1(1)	1(1)	
Polycent (*Neureclipsis*)	3, 1, 4	4, 2, 4	8	3(1)	3(1)	CF,SHH,Pred
Other Trichop (*Nectopsyche*)	1, 0, 3	1, 0, 3	4	1(1)	1(1)	SHH/CG
Other	1, 0, 2	1, 0, 2	3	1(1)	1(1)	
Acariformes	1, 0, 0	1, 0, 0	1	<1(1)	<1(1)	Pred
Hydra	0, 0, 1	0, 0, 1	1	<1(1)	<1(<1)	Pred
Planariidae	0, 0, 1	0, 0, 1	1	<1(1)	<1(<1)	Pred,CG
Oligochaeta	2, 7, 16	3, 12, 15	25	8(7)	10(6)	CG
Zooplankton	21, 4, 17	29, 7, 16	42	14(9)	17(11)	
Cladocera	2, 1, 1	3, 2, 1	4	1(1)	2(1)	
Bosmina	1, 0, 1	1, 0, 1	2	1(<1)	1(1)	CF
Daphnia	1, 1, 0	1, 2, 0	2	1(<1)	1(1)	CF
Copepoda (Cyclopoida)	18, 3, 16	25, 5, 15	37	12(8)	15(10)	Pred
Ostracoda	1, 0, 0	1, 0, 0	1	<1(1)	<1(1)	CF

Taxa WND7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	149, 196, 120		465	155(38)		
Chironomidae	49, 34, 26	33, 17, 22	109	36(12)	24(8)	Mainly CG
Total other Insecta	68, 59, 48	46, 30, 40	175	58(10)	39(8)	
Coleoptera (Elmidae) larvae	0, 1, 1	0, <1, 1	2	1(1)	<1(<1)	CG,Scr
Collembola	1, 1, 0	1, <1, 0	2	1(1)	<1(<1)	CG
Other Diptera	8, 4, 5	5, 2, 4	17	6(2)	4(2)	
Ceratopogonidae	1, 2, 0	1, 1, 0	3	1(1)	1(<1)	CG,Pred
Empididae (*Hemerodromia*)	2, 0, 0	1, 0, 0	2	1(1)	<1(1)	Pred, CG
Simuliidae (*Simulium*)	2, 1, 5	1, <1, 4	8	3(2)	2(2)	CF
Stratiomyidae	1, 1, 0	1, <1, 0	2	1(1)	<1(<1)	CG
Unknown	2, 0, 0	1, 0, 0	2	1(1)	<1(1)	
Ephemeroptera	21, 19, 30	14, 10, 25	70	23(6)	16(8)	
Baetidae (*Baetis*)	3, 1, 3	2, <1, 2	7	2(1)	2(1)	CG,Scr
Caenidae (*Caenis*)	9, 8, 4	6, 4, 3	21	7(3)	4(1)	CG,Scr
Heptageniidae (*Stenonema*)	9, 9, 23	6, 5, 19	41	14(8)	10(8)	Scr,CG
Tricoryithidae (*Tricorythodes*)	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	CG
Hymenoptera	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	parasite
Plecoptera (*Isoperla*)	12, 4, 5	8, 2, 4	21	7(4)	5(3)	Pred,CG
Trichoptera	26, 29, 7	17, 15, 6	62	21(12)	13(6)	
Hydropsychidae	19, 15, 3	13, 8, 2	37	12(8)	8(5)	CF
H. bidens	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	
H. orris	16, 11, 3	11, 6, 2	30	10(7)	6(4)	
H. simulans	1, 1, 0	1, <1, 0	2	1(<1)	<1(<1)	
P. flava	2, 2, 0	1, 1, 0	4	1(1)	1(1)	
Polycent (*Neureclipsis*)	0, 4, 0	0, 2, 0	4	1(2)	1(1)	CF,SHH,Pred
Other Trichoptera	7, 10, 4	5, 5, 2	21	7(3)	4(2)	
Brachycentrus	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	CF,Scr
Nectopsyche	6, 6, 3	4, 3, 2	15	5(2)	3(1)	SHH,CG

WND7 (Cont.) Table 6 (9 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Triaenodes	1, 3, 1	1, 1, 1	5	2(1)	1(<1)	SHH
Other	1, 7, 5	1, 4, 4	13	4(3)	3(2)	
Acariformes	0, 2, 0	0, 1, 0	2	1(1)	<1(1)	Pred
Amphipoda (*H. azteca*)	1, 4, 4	1, 2, 3	9	3(2)	2(1)	CG (poss SH)
Isopoda (*Asellus*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(<1)	CG (poss SH)
Pseudoscorpiones	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	Pred
Oligochaeta	14, 29, 20	9, 15, 17	63	21(8)	14(4)	CG
Zooplankton	17, 67, 21	11, 34, 17	105	35(28)	21(12)	
Cladocera (*Daphnia*)	1, 1, 1	1, <1, 1	3	1(0)	1(<1)	CF
Copepoda (Cyclopoida)	16, 61, 18	11, 31, 15	95	32(25)	19(11)	Pred
Nematoda	0, 4, 2	0, 2, 2	6	2(2)	1(1)	CG
Ostracoda	0, 1, 0	0, <1, 0	1	<1(1)	<1(<1)	CF

Taxa WND30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	268, 2, 211		481	160(140)		
Chironomidae	16, 1, 29	6, 50, 14	46	15(14)	23(23)	Mainly CG
Total other Insecta	88, 1, 87	33, 50, 41	176	59(50)	41(9)	
Coleoptera (Elmidae) adult	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	CG,Scr
Collembola	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG
Other Diptera	65, 1, 21	24, 50, 10	87	29(33)	28(20)	
Empidid (*Hemerodromia*)	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred,CG
Simuliidae (*Simulium*)	63, 0, 19	23, 0, 9	82	27(32)	11(12)	CF
Unknown	1, 1, 2	<1, 50, 1	4	1(1)	17(28)	
Ephemeroptera	15, 0, 49	6, 0, 23	64	21(25)	10(12)	
Baetidae (*Baetis*)	6, 0, 1	2, 0, <1	7	2(3)	1(1)	CG,Scr
Caenidae (*Caenis*)	3, 0, 27	1, 0, 13	30	10(15)	5(7)	CG,Scr
Heptageniidae (*Stenonema*)	5, 0, 21	2, 0, 10	26	9(11)	4(5)	Scr,CG
Tricoryithidae (*Tricorythodes*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG
Unknown	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	
Plecoptera (*Isoperla*)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	Pred,CG
Trichoptera	7, 0, 14	3, 0, 7	21	7(7)	3(3)	
Hydropsychidae (*H. orris*)	2, 0, 5	1, 0, 2	7	2(2)	1(1)	CF
Other Trich (*Nectopsyche*)	5, 0, 9	2, 0, 4	14	5(4)	2(2)	SHH,CG
Zygoptera (Coenagrionidae)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	Pred
Other	87, 0, 67	32, 0, 32	154	51(46)	21(18)	
Acariformes	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred
Amphipoda (*H. azteca*)	58, 0, 12	22, 0, 6	70	23(31)	9(11)	CG (poss SH)
Decapoda (crayfish)	0, 0, 1	0, 0, <1	1	<1(1)	<1(<1)	CG,SHH
Hydra	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred
Isopoda (*Asellus*)	24, 0, 53	9, 0, 25	77	26(26)	11(13)	CG (poss SH)
Physidae (*Physa*)	2, 0, 1	1, 0, <1	3	1(1)	<1(<1)	Scr,CG (poss SH)
Planariidae	1, 0, 0	<1, 0, 0	1	<1(1)	<1(<1)	Pred,CG
Oligochaeta	40, 0, 8	15, 0, 4	48	16(21)	6(8)	CG
Zooplankton	37, 0, 19	14, 0, 9	56	19(18)	8(7)	
Cladocera	4, 0, 3	1, 0, 1	7	2(2)	1(1)	
Bosmina	2, 0, 1	1, 0, <1	3	1(1)	<1(<1)	CF
Daphnia	2, 0, 2	1, 0, 1	4	1(1)	1(<1)	CF
Copepoda (Cyclopoida)	30, 0, 13	11, 0, 6	43	14(15)	6(6)	Pred
Nematoda	2, 0, 2	1, 0, 1	4	1(1)	1(<1)	CG
Ostracoda	1, 0, 1	<1, 0, <1	2	1(1)	<1(<1)	CF

Table 6 (10 of 14)

Taxa AWND2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	58, 76, 97		231	77(19)		
Chironomidae	10, 20, 28	17, 26, 29	58	19(9)	24(6)	Mainly CG
Total other Insecta	12, 19, 46	21, 25, 47	77	26(18)	31(14)	
Coleoptera (Elmidae) larvae	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	CG,Scr
Other Diptera	0, 4, 1	0, 5, 1	5	2(2)	2(3)	
Empidid (*Hemerodromia*)	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	Pred,CG
Simuliidae (*Simulium*)	0, 3, 1	0, 4, 1	4	1(1)	2(2)	CF
Ephemeroptera	5, 6, 17	9, 8, 17	28	9(7)	11(5)	
Baetidae (*Baetis*)	0, 0, 3	0, 0, 3	3	1(2)	1(2)	CG,Scr
Caenidae (*Caenis*)	3, 4, 7	5, 5, 7	14	5(2)	6(1)	CG,Scr
Heptageniidae (*Stenonema*)	2, 1, 6	3, 1, 6	9	3(3)	4(2)	Scr,CG
Tricoryithidae (*Tricorythodes*)	0, 1, 1	0, 1, 1	2	1(1)	1(1)	CG
Hemiptera (Corixidae)	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	PH,Pred,Scr
Plecoptera (*Isoperla*)	1, 0, 1	2, 0, 1	2	1(1)	1(1)	Pred,CG
Trichoptera	6, 7, 27	10, 9, 28	40	13(12)	16(10)	
Hydropsychidae	4, 4, 17	7, 5, 17	25	8(7)	10(7)	CF
H. orris	4, 3, 12	7, 4, 12	19	6(5)	8(4)	
H. simulans	0, 0, 3	0, 0, 3	3	1(2)	1(2)	
P. flava	0, 1, 2	0, 1, 2	3	1(1)	1(1)	
Polycent (*Neureclipsis*)	2, 1, 3	3, 1, 3	6	2(1)	3(1)	CF,SHH,Pred
Other Trich (*Nectopsyche*)	0, 2, 7	0, 3, 7	9	3(4)	3(4)	SHH,CG
Other	2, 1, 2	3, 1, 2	5	2(1)	2(1)	
Amphipoda (*H. azteca*)	0, 0, 2	0, 0, 2	2	1(1)	1(1)	CG (poss SH)
Hydra	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	Pred
Isopoda (*Asellus*)	2, 0, 0	3, 0, 0	2	1(1)	1(2)	CG (poss SH)
Oligochaeta	18, 16, 11	31, 21, 11	45	15(4)	21(10)	CG
Zooplankton	16, 20, 10	28, 26, 10	46	15(5)	21(10)	
Copepoda	12, 18, 10	21, 24, 10	40	13(4)	18(7)	
Calanoid	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CF
Cyclopoida	12, 18, 9	21, 24, 9	39	13(5)	18(8)	Pred
Cladocera	3, 2, 0	5, 3, 0	5	2(1)	3(3)	
Bosmina	2, 2, 0	3, 3, 0	4	1(1)	2(2)	CF
Daphnia	1, 0, 0	2, 0, 0	1	<1(1)	1(1)	CF
Ostracoda	1, 0, 0	2, 0, 0	1	<1(1)	1(1)	CF

Taxa AWND7	N (r = 2)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	57, 82		139	69(18)		
Chironomidae	9, 20	16, 24	29	14(8)	20(6)	Mainly CG
Total other Insecta	26, 29	46, 35	55	27(2)	40(7)	
Coleoptera	0, 2	0, 2	2	1(1)	1(2)	
Elmidae larvae	0, 1	0, 1	1	<1(1)	1(1)	CG,Scr
Staphylinidae adult	0, 1	0, 1	1	<1(1)	1(1)	Pred
Other Diptera (*Simulium*)	6, 1	10, 1	7	3(3)	6(7)	CF
Ephemeroptera	15, 15	26, 18	30	15(0)	22(6)	
Baetidae (*Baetis*)	5, 2	9, 2	7	3(2)	6(4)	CG,Scr
Caenidae (*Caenis*)	2, 5	3, 6	7	3(2)	5(2)	CG,Scr
Heptageniidae (*Stenonema*)	8, 6	14, 7	14	7(1)	11(5)	Scr,CG
Tricoryithidae (*Tricorythodes*)	0, 2	0, 2	2	1(1)	1(2)	CG
Plecoptera (*Isoperla*)	2, 2	3, 2	4	2(0)	3(1)	Pred,CG
Trichoptera	3, 9	5, 11	12	6(4)	8(4)	
Hydropsychidae (*H. orris*)	1, 0	2, 0	1	<1(1)	1(1)	CF
Polycent (*Neureclipsis*)	0, 2	0, 2	2	1(1)	1(2)	CF,SHH,Pred

AWND7 (Cont.) Table 6 (11 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Other Trichoptera	2, 7	3, 8	9	4(3)	6(4)	
Nectopsyche	0, 7	0, 8	7	3(5)	4(6)	SHH,CG
Triaenodes	2, 0	3, 0	2	1(1)	2(2)	SHH
Other	5, 3	9, 4	8	4(1)	6(4)	
Acariformes	1, 0	2, 0	1	<1(1)	1(1)	Pred
Amphipoda (*H. azteca*)	2, 2	3, 2	4	2(0)	3(1)	CG (poss SH)
Aranae	1, 0	2, 0	1	<1(1)	1(1)	Pred
Isopoda (*Asellus*)	1, 0	2, 0	1	<1(1)	1(1)	CG (poss SH)
Physidae (*Physa*)	0, 1	0, 1	1	<1(1)	1(1)	Scr,CG,(poss SH)
Oligochaeta	10, 18	17, 22	28	14(6)	20(3)	CG
Zooplankton	7, 12	12, 15	19	9(3)	13(2)	
Cladocera (*Daphnia*)	0, 1	0, 1	1	<1(1)	1(1)	CF
Copepoda (Cyclopoida)	5, 8	9, 10	13	6(2)	9(1)	Pred
Nematoda	2, 3	3, 4	5	2(1)	4(<1)	CG

Taxa AWND30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	18, 3, 14		35	12(8)		
Chironomidae	14, 1, 4	78, 33, 29	19	6(7)	47(27)	Mainly CG
Total other Insecta	2, 0, 4	11, 0, 29	6	2(2)	13(14)	
Other Diptera	2, 0, 2	11, 0, 14	4	1(1)	8(7)	
Ceratopogonidae	2, 0, 0	11, 0, 0	2	1(1)	4(6)	CG,Pred
Empidid (*Hemerodromia*)	0, 0, 1	0, 0, 7	1	<1(1)	2(4)	Pred,CG
Tipulidae	0, 0, 1	0, 0, 7	1	<1(1)	2(4)	SHD,CG
Unknown insect	0, 0, 2	0, 0, 14	2	1(1)	5(8)	
Other	0, 0, 4	0, 0, 29	4	1(2)	9(16)	
Acariformes	0, 0, 3	0, 0, 21	3	1(2)	7(12)	Pred
Amphipoda (*H. azteca*)	0, 0, 1	0, 0, 7	1	<1(1)	2(4)	CG (poss SH)
Oligochaeta	1, 2, 2	6, 67, 14	5	2(1)	29(33)	CG
Zooplankton (Cyclopoida)	1, 0, 0	6, 0, 0	1	<1(1)	2(3)	Pred

Taxa LND2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	24, 32, 76		132	44(28)		
Chironomidae	7, 5, 15	29, 16, 20	27	9(5)	21(7)	Mainly CG
Total other Insecta	11, 12, 33	46, 37, 43	56	19(12)	42(4)	
Other Diptera	5, 0, 3	21, 0, 4	8	3(2)	8(11)	
Empidid (*Hemerodromia*)	1, 0, 0	4, 0, 0	1	<1(1)	1(2)	Pred,CG
Simuliidae (*Simulium*)	4, 0, 3	17, 0, 4	7	2(2)	7(9)	CF
Ephemeroptera	2, 2, 4	8, 6, 5	8	3(1)	7(2)	
Baetidae (*Baetis*)	2, 1, 2	8, 3, 3	5	2(1)	5(3)	CG,Scr
Caenidae (*Caenis*)	0, 1, 2	0, 3, 3	3	1(1)	2(2)	CG,Scr
Plecoptera (*Isoperla*)	1, 0, 6	4, 0, 8	7	2(3)	4(4)	Pred,CG
Trichoptera	3, 10, 20	12, 31, 26	33	11(8)	23(10)	
Hydropsychidae	2, 7, 14	8, 22, 18	23	8(6)	16(7)	CF
H. orris	0, 5, 13	0, 16, 17	18	6(7)	11(9)	
H. simulans	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	
P. flava	2, 1, 1	8, 3, 1	4	1(1)	4(4)	
Polycent (*Neureclipsis*)	1, 1, 4	4, 3, 5	6	2(2)	4(1)	CF,SHH,Pred
Other Trich (*Nectopsyche*)	0, 2, 2	0, 6, 3	4	1(1)	3(3)	SHH,CG
Other	0, 2, 3	0, 6, 4	5	2(1)	3(3)	
Acariformes	0, 2, 0	0, 6, 0	2	1(1)	2(4)	Pred
Amphipoda (*H. azteca*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CG (poss SH)
Isopoda (*Asellus*)	0, 0, 2	0, 0, 3	2	1(1)	1(1)	CG (poss SH)
Oligochaeta	0, 11, 10	0, 34, 13	21	7(6)	16(17)	CG

LND2 (Cont.) Table 6 (12 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Zooplankton	6, 2, 15	25, 6, 20	23	8(7)	17(10)	
Cladocera	1, 0, 3	4, 0, 4	4	1(1)	3(2)	
Bosmina	0, 0, 2	0, 0, 3	2	1(1)	1(1)	CF
Daphnia	1, 0, 1	4, 0, 1	2	1(1)	2(2)	CF
Copepoda (Cyclopoida)	4, 2, 10	17, 6, 13	16	5(4)	12(5)	Pred
Nematoda	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CG
Ostracoda	1, 0, 1	4, 0, 1	2	1(1)	2(2)	CF

Taxa LND7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	17, 87, 75		179	60(37)		
Chironomidae	4, 32, 24	23, 37, 32	60	20(14)	31(7)	Mainly CG
Total other Insecta	0, 17, 8	0, 19, 11	25	8(8)	10(10)	
Coleoptera (unknown)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	
Collembola	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	CG
Other Diptera (*Simulium*)	0, 2, 0	0, 2, 0	2	1(1)	1(1)	CF
Ephemeroptera	0, 9, 4	0, 10, 5	13	4(4)	5(5)	
Baetidae (*Baetis*)	0, 2, 2	0, 2, 3	4	1(1)	2(1)	CG,Scr
Caenidae (*Caenis*)	0, 2, 1	0, 2, 1	3	1(1)	1(1)	CG,Scr
Heptageniidae (Stenonema)	0, 5, 1	0, 6, 1	6	2(3)	2(3)	Scr,CG
Hemiptera (unknown)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	PH,Pred,Scr
Plecoptera (*Isoperla*)	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	Pred,CG
Trichoptera (*Nectopsyche*)	0, 4, 2	0, 5, 3	6	2(2)	2(2)	SHH,CG
Other	1, 2, 3	6, 2, 4	6	2(1)	4(2)	
Acariformes	1, 1, 0	6, 1, 0	2	1(1)	2(3)	Pred
Amphipoda (*H. azteca*)	0, 1, 1	0, 1, 1	2	1(1)	1(1)	CG (poss SH)
Hydra	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	Pred
Isopoda (*Asellus*)	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CG (poss SH)
Oligochaeta	4, 24, 23	23, 28, 31	51	17(11)	27(4)	CG
Zooplankton	8, 12, 17	47, 14, 23	37	12(4)	28(17)	
Cladocera	0, 3, 2	0, 3, 3	5	2(1)	2(2)	
Bosmina	0, 0, 1	0, 0, 1	1	<1(1)	<1(1)	CF
Daphnia	0, 3, 1	0, 3, 1	4	1(1)	2(2)	CF
Copepoda (Cyclopoida)	8, 9, 15	47, 10, 20	32	11(4)	26(19)	Pred

Taxa LND30	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	4, 35, 1		40	13(19)		
Chironomidae	0, 5, 0	0, 14, 0	5	2(3)	5(8)	Mainly CG
Other Diptera (*Simulium*)	0, 2, 0	0, 6, 0	2	1(1)	2(3)	CF
Other	0, 5, 1	0, 14, 100	6	2(3)	38(54)	
Aranae	0, 0, 1	0, 0, 100	1	<1(1)	33(58)	Pred
Isopoda (*Asellus*)	0, 4, 0	0, 11, 0	4	1(2)	4(7)	CG,(poss SH)
Physidae (*Physa*)	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	Scr,CG,(poss SH)
Oligochaeta	1, 14, 0	25, 40, 0	15	5(8)	22(20)	CG
Zooplankton	3, 8, 0	75, 23, 0	11	4(4)	33(38)	
Cladocera	2, 2, 0	50, 6, 0	4	1(1)	19(27)	
Bosmina	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	CF
Daphnia	2, 1, 0	50, 3, 0	3	1(1)	18(28)	CF
Copepoda (Cyclopoida)	1, 6, 0	25, 17, 0	7	2(3)	14(13)	Pred
Minnow (fry)	0, 1, 0	0, 3, 0	1	<1(1)	1(2)	

Table 6 (13 of 14)

Taxa ALND2	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	8, 77, 15		100	33(38)		
Chironomidae	0, 9, 7	0, 12, 47	16	5(5)	19(24)	Mainly CG
Total other Insecta	3, 25, 3	37, 32, 20	31	10(13)	30(9)	
Other Diptera	2, 4, 0	25, 5, 0	6	2(2)	10(13)	
Chaoboridae (*Chaoborus*)	1, 0, 0	12, 0, 0	1	<1(1)	4(7)	Pred
Simuliidae (*Simulium*)	0, 3, 0	0, 4, 0	3	1(2)	1(2)	CF
Tipulidae	1, 1, 0	12, 1, 0	2	1(1)	5(7)	SHD,CG
Ephemeroptera	0, 10, 0	0, 13, 0	10	3(6)	4(7)	
Baetidae (*Baetis*)	0, 6, 0	0, 8, 0	6	2(3)	3(4)	CG,Scr
Heptageniidae (*Stenonema*)	0, 4, 0	0, 5, 0	4	1(2)	2(3)	Scr,CG
Trichoptera	1, 11, 3	12, 14, 20	15	5(5)	16(4)	
Hydropsychidae	1, 8, 3	12, 10, 20	12	4(4)	14(5)	CF
H. orris	1, 6, 3	12, 8, 20	10	3(2)	13(6)	
H. simulans	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	
P. flava	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	
Polycent (*Neureclipsis*)	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	CF,SHH,Pred
Other Trich (*Nectopsyche*)	0, 2, 0	0, 3, 0	2	1(1)	1(1)	SHH,CG
Other	0, 3, 0	0, 4, 0	3	1(2)	1(2)	
Acariformes	0, 2, 0	0, 3, 0	2	1(1)	1(1)	Pred
Physidae (*Physa*)	0, 1, 0	0, 1, 0	1	<1(1)	<1(1)	Scr,CG, (poss SH)
Oligochaeta	0, 9, 4	0, 12, 27	13	4(4)	13(13)	CG
Zooplankton	5, 31, 1	62, 40, 7	37	12(16)	36(28)	
Cladocera	2, 0, 0	25, 0, 0	2	1(1)	8(14)	
Bosmina	1, 0, 0	12, 0, 0	1	<1(1)	4(7)	CF
Daphnia	1, 0, 0	12, 0, 0	1	<1(1)	4(7)	CF
Copepoda	3, 28, 1	37, 36, 7	32	11(15)	27(17)	
Calanoida	0, 2, 0	0, 3, 0	2	1(1)	1(1)	CF
Cyclopoida	3, 26, 1	37, 34, 7	30	10(14)	26(17)	Pred
Nematoda	0, 3, 0	0, 4, 0	3	1(2)	1(2)	CG

Taxa ALND7	N (r = 3)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	105, 170, 100		375	125(39)		
Chironomidae	24, 25, 15	23, 15, 15	64	21(5)	17(5)	Mainly CG
Total other Insecta	22, 54, 16	21, 32, 16	92	31(20)	23(8)	
Coleop (Elmidae) adult/larvae	0, 1, 1	0, 1, 1	2	1(<1)	<1(<1)	CG,Scr
Collembola	0, 2, 0	0, 1, 0	2	1(1)	<1(1)	CG
Other Diptera	2, 8, 0	2, 5, 0	10	3(4)	2(2)	
Culicidae	0, 1, 0	0, 1, 0	1	<1(1)	<1(<1)	CF,CG
Empidid (*Hemerodromia*)	1, 1, 0	1, 1, 0	2	1(1)	<1(<1)	Pred,CG
Simuliidae (*Simulium*)	1, 6, 0	1, 3, 0	7	2(3)	1(2)	CF
Ephemeroptera	13, 27, 5	12, 16, 5	45	15(11)	11(6)	
Baetidae (*Baetis*)	0, 4, 0	0, 2, 0	4	1(2)	1(1)	CG,Scr
Caenidae (*Caenis*)	8, 2, 4	8, 1, 4	14	5(3)	4(3)	CG,Scr
Heptageniidae (*Stenonema*)	4, 21, 0	4, 12, 0	25	8(11)	5(6)	Scr,CG
Tricoryithidae (*Tricorythodes*)	1, 0, 1	1, 0, 1	2	1(1)	1(1)	CG
Plecoptera (*Isoperla*)	1, 5, 2	1, 3, 2	8	3(2)	2(1)	Pred,CG
Trichoptera	5, 10, 7	5, 6, 7	22	7(2)	6(1)	
Hydropsychidae (*H. orris*)	1, 2, 0	1, 1, 0	3	1(1)	1(1)	CF
Polycent (*Neureclipsis*)	1, 1, 2	1, 1, 2	4	1(1)	1(1)	CF,SHH,Pred
Other Trichoptera	3, 7, 5	3, 4, 5	15	5(2)	4(1)	
Nectopsyche	3, 6, 4	3, 3, 4	13	4(1)	3(1)	SHH,CG
Triaenodes	0, 1, 1	0, 1, 1	2	1(1)	<1(<1)	SHH
Unknown (earwig?)	1, 1, 1	1, 1, 1	3	1(0)	1(<1)	

ALND7 (Cont.) Table 6 (14 of 14)

Taxa	N	N (%)	Total	Mean	Mean %	FF Group
Other	7, 7, 7	7, 4, 7	21	7(0)	6(2)	
Acariformes	3, 2, 1	3, 1, 1	6	2(1)	2(1)	Pred
Amphipoda (*H. azteca*)	0, 4, 4	0, 2, 4	8	3(2)	2(2)	CG (poss SH)
Isopoda (*Asellus*)	3, 1, 2	3, 1, 2	6	2(1)	2(1)	CG (poss SH)
Physidae (*Physa*)	1, 0, 0	1, 0, 0	1	<1(1)	<1(1)	Scr,CG,(poss SH)
Oligochaeta	26, 19, 14	25, 11, 14	59	20(6)	17(7)	CG
Zooplankton	26, 65, 48	25, 38, 48	139	46(20)	37(12)	
Cladocera	2, 6, 0	2, 3, 0	8	3(3)	2(2)	
Bosmina	1, 1, 0	1, 1, 0	2	1(1)	<1(<1)	CF
Daphnia	1, 5, 0	1, 13, 0	6	2(3)	1(1)	CF
Copepoda	24, 57, 47	23, 33, 47	128	43(17)	34(12)	
Calanoida	0, 1, 1	0, 1, 1	2	1(1)	<1(<1)	CF
Cyclopoida	24, 56, 46	23, 33, 46	126	42(16)	34(12)	Pred
Nematoda	0, 2, 1	0, 1, 1	3	1(1)	1(1)	CG

Taxa ALND30	N (r = 4)	N (%)	Total N	Mean (sd)	Mean % (sd)	FF Group
Total Invertebrates	31, 11, 9, 7		58	14(11)		
Chironomidae	1, 11, 3, 1	3, 100, 33, 14	16	4(5)	38(43)	Mainly CG
Total other Insecta	12, 0, 1, 5	39, 0, 11, 71	18	4(5)	30(32)	
Other Diptera	8, 0, 0, 4	26, 0, 0, 57	12	3(4)	21(27)	
Ceratopogonidae	0, 0, 0, 1	0, 0, 0,14	1	<1(<1)	4(7)	CG,Pred
Simuliidae (*Simulium*)	8, 0, 0, 3	26, 0, 0, 43	11	3(4)	17(21)	CF
Ephemeroptera	3, 0, 1, 0	10, 0, 11, 0	4	1(1)	5(6)	
Baetidae (*Baetis*)	2, 0, 0, 0	6, 0, 0, 0	2	<1(1)	2(3)	CG,Scr
Heptageniidae (*Stenonema*)	1, 0, 1, 0	3, 0, 11, 0	2	<1(1)	4(5)	Scr,CG
Plecoptera (*Isoperla*)	0, 0, 0, 1	0, 0, 0, 14	1	<1(<1)	4(7)	Pred,CG
Trichoptera (*H. orris*)	1, 0, 0, 0	3, 0, 0, 0	1	<1(<1)	1(2)	CF
Other	2, 0, 2, 0	6, 0, 22, 0	4	1(1)	7(10)	
Amphipoda (*H. azteca*)	1, 0, 1, 0	3, 0, 11, 0	2	<1(1)	4(5)	CG (poss SH)
Isopoda (*Asellus*)	1, 0, 1, 0	3, 0, 11, 0	2	<1(1)	4(5)	CG (poss SH)
Oligochaeta	1, 0, 3, 0	3, 0, 33, 0	4	1(1)	9(16)	CG
Zooplankton	15, 0, 0, 0	48, 0, 0, 0	15	4(7)	12(24)	
Cladocera (*Daphnia*)	2, 0, 0, 0	6, 0, 0, 0	2	<1(1)	2(3)	CF
Copepoda (Cyclopoida)	9, 0, 0, 0	29, 0, 0, 0	9	2(4)	7(14)	Pred
Nematoda	1, 0, 0, 0	3, 0, 0, 0	1	<1(<1)	1(2)	CG
Ostacoda	3, 0, 0, 0	10, 0, 0, 0	3	1(1)	2(5)	CF
Minnow (fry)	0, 0, 0, 1	0, 0, 0, 14	1	<1(<1)	4(7)	

2.6.4. Appendix C

Invertebrate Tolerance Values and Biotic Indices

Table 2. Tolerance values (TV) used for Missouri River Invertebrates. Values from Pruess (unpub) and *Resh et al. (1996).

Taxa	TV	Taxa (cont.)	TV
Chironomidae		Ephemeroptera	
Chironomini (blood worm midges)*	8	Heptageniidae*	4
Chironomus	10	*Stenonema*	4
Cryptochironomus	8	Caenidae	7
Dicrotendipes	8	*Caenis*	7
Endochironomus	10	Baetidae	
Glypotendipes	10	*Baetis*	4
Parachironomus	8	Tricorythidae*	4
Phaenopsectra	7	*Tricorythodes*	5
Polypedilum	8	Other Diptera	
Other chironomids*	6	Simuliidae*	6
Orthocladinae		Tipulidae	6
Cardiocladius	4	Ceratopogonidae	7
Corynoneura	4	*Chaoborus*	7
Cricotopus	7	Empididae	6
Diplocladius	4	Plecoptera	
Eukiefferiella	5	Perlodidae*	2
Hydrobaenus	7	Coleoptera	
Nanocladius	4	Elmidae	5
Orthocladius	5	Haliplidae	8
Paraphaenocladius	4	Other Coleoptera	5
Rheocricotopus	6		
Thienemanniella	6	Non-Insecta	
Tanypoda		Acariformes*	4
Ablabesmyia	6	*Asellus*	6
Larsia	6	Coenagrionidae	7
Procladius	9	Decapoda*	6
Tanytarsini		*Hyallela*	8
Cladotanytarsus	6	Oligochaeta*	8
Paratanytarsus	6	Physidae*	8
Pseudochironomus	5		
Odontomesa	2		
Trichoptera			
Hydropsychidae*	4		
Hydropsyche simulans	7		
Cheumatopsyche	5		
Potamyia	5		
Polycentropodidae*	6		
Polycentropus	4		
Hydroptilidae	6		
Leptoceridae*	4		
Nectopsyche	5		
Brachycentropodidae	1		
Brachycentrus	1		

Rating

< 3.5 = excellent water quality *

7 = poor water quality

0 = clean water only

10 = extreme pollution tolerance

Table 3. Mean (±SD) of Biotic Indices calculated from taxa colonizing substrates on days 2, 7, 30, and 60, as in Hilsenhoff (1988) in Resh et al. (1996). Overall values, combining all treatments per day is included.

		Biotic Index Values			
site	trt	d2	d7	d30	d60
SB	L	6.51(0.30)	6.22(0.38)	7.11(0.30)	7.17 (r=1)
	AL	6.39(0.23)	6.59(0.40)	6.93(0.21)	6.50(0.07)
	W	6.35(0.08)	6.35(0.26)	6.79(0.13)	6.60(0.15)
	AW	6.44(0.22)	6.29(0.25)	6.88(0.08)	6.43(0.79)
	combined treatments	6.42(0.20)	6.36(0.32)	6.93(0.21)	6.60(0.42)
N	L	5.66(0.50)	6.68(0.10)	7.77(0.33)	*
	AL	5.90(0.46)	6.23(0.54)	6.67(1.18)	*
	W	5.25(0.36)	5.76(0.30)	6.36(0.31)	*
	AW	6.35(0.40)	6.16(0.25)	7.50(0.87)	*
	combined treatments	5.79(0.56)	6.21(0.46)	6.98(0.93)	*

* N substrates not available on day 60.

Water quality based on biotic index values; developed for use on Wisconsin streams to determine the degree of organic pollution, thresholds may differ regionally.

Family biotic index	Water quality
0.00 – 3.75	Excellent
3.76 – 4.25	Very good
4.26 – 5.00	Good
5.01 – 5.75	Fair
5.76 – 6.50	Fairly poor
6.51 – 7.25	Poor
7.26 – 10.00	Very poor

Table 4. Biotic Index values derived from communities colonizing substrates at SB (upstream) and N (downstream) and their implications on "water quality" or substrate condition, as in Hilsenhoff (1988) in Resh et al. (1996).

Site	Trt	Day	Biotic Index	Implication (Range)	Mean (sd)	Implication (of mean)
SB	L	2	6.27, 6.40, 6.85,	Fairly poor – poor	6.51 (0.30)	Poor
	L	7	5.90, 6.12, 6.64	Fairly poor – poor	6.22 (0.38)	Fairly poor
	L	30	6.80, 7.14, 7.39	Poor – very poor	7.11 (0.30)	Poor
	L	60	7.17	Poor		Poor
	AL	2	6.50, 6.53, 6.12	Fairly poor - poor	6.39 (0.23)	Fairly poor
	AL	7	6.26, 6.47, 7.03	Fairly poor - poor	6.59 (0.40)	Poor
	AL	30	6.80, 6.83, 7.17	Poor	6.93 (0.21)	Poor
	AL	60	6.45, 6.55	Fairly poor - poor	6.50 (0.07)	Fairly poor
	W	2	6.25, 6.39, 6.40	Fairly poor	6.35 (0.08)	Fairly poor
	W	7	6.09, 6.36, 6.61	Fairly poor - poor	6.35 (0.26)	Fairly poor
	W	30	6.66, 6.79, 6.91	Poor	6.79 (0.13)	Poor
	W	60	6.49, 6.70	Fairly poor - poor	6.60 (0.15)	Poor
	AW	2	6.23, 6.42, 6.67	Fairly poor - poor	6.44 (0.22)	Fairly poor
	AW	7	6.07, 6.23, 6.56	Fairly poor - poor	6.29 (0.25)	Fairly poor
	AW	30	6.81, 6.87, 6.97	Poor	6.88 (0.08)	Poor
	AW	60	5.87, 6.99	Fairly poor - poor	6.43 (0.79)	Fairly poor
N	L	2	5.28, 5.46, 6.23	Fair – fairly poor	5.66 (0.50)	Fair
	L	7	6.59, 6.67, 6.79	Poor	6.68 (0.10)	Poor
	L	30	7.54, 8.00	Very poor	7.77 (0.33)	Very poor
	AL	2	5.61, 5.67, 6.43	Fair – fairly poor	5.90 (0.46)	Fairly poor
	AL	7	5.61, 6.51, 6.57	Fair – poor	6.23 (0.54)	Fairly poor
	AL	30	5.60, 5.75, 7.33, 8.00	Fair – very poor	6.67 (1.18)	Poor
	W	2	4.84, 5.37, 5.53	Good – fair	5.25 (0.36)	Fair
	W	7	5.47, 5.74, 6.06	Fair – fairly poor	5.76 (0.30)	Fairly poor
	W	30	6.00, 6.50, 6.57	Fairly poor – poor	6.36 (0.31)	Fairly poor
	AW	2	5.91, 6.46, 6.69	Fairly poor – poor	6.35 (0.40)	Fairly poor
	AW	7	5.98, 6.33	Fairly poor	6.16 (0.25)	Fairly poor
	AW	30	6.50, 8.00, 8.00	Fairly poor – very poor	7.50 (0.87)	Very poor

2.6.5. Appendix D

Invertebrate Gut Contents

Table 1. ANOVA for effects of substrate, time and site on gut contents of a) Chironomidae and b) Trichoptera. No Trichoptera were collected from L-N and AW-N substrates on day 30.

(a) Chironomidae

Substrate effects					Effects of time (d)				Site effects			
gut content	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Cottonwood	SB	30	W > AW	0.03	SB	W	d30 > d60	0.02	2	AW	N > SB	0.03
Biofilm	SB	7	W > L	0.00	SB	L, AL	d30,60 > d7	0.00, 0.00	2	All trts	N > SB	0.00 each
		7	AW > AL	0.00	SB	W, AW	d7,30,60 > d2	0.00, 0.00, 0.00	7	L, AL	N > SB	0.00, 0.00
Fiber					SB	L, AL	d7 > d2	0.04, 0.05	2	W, AW	N > SB	0.00, 0.00
						AW	d30 > d7	0.04	7	W, AW	N > SB	0.02, 0.00
						AW	d60 > d30	0.02				
Animal					SB	W	d60 > d30	0.02				
Diatoms	N	7	W > L	0.03	SB	W, AW	d2,7 > d30,60	0.00 each	2,7	All trts	SB > N	0.00
						AW	d60 > d30	0.00				
						AL	d2,7 > d30,60	0.00 each				
						L	d7 > d2,30,60	0.00, 0.00, 0.00				
Desmids					SB	W	d30 > d60	0.01				

(b) Trichoptera (cont. on following page)

Substrate effects					Effects of time (d)				Site effects			
gut content	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Cottonwood	SB	7	L > AL	0.03	SB	AW	d7 > d30	0.00				
		7	AW > W	0.01								
		7	AW > AL	0.00								
Biofilm	SB	2	AL > AW	0.02	SB	L	d30 > d60	0.03				
		7	W > L	0.03	N	AW, L	d2 > d7	0.01, 0.00				
		60	AW > AL	0.01								
	N	2	AL > AW	0.00								
		7	W > AW	0.03								
		7	W > L	0.01								
Fiber	N	2	AL >L	0.05	SB	L	d7 > d2,30	0.02, 0.02	2	L	N > SB	0.02
		2	AL > AW	0.05	N	AW, AL	d2 > d7	0.01, 0.00				
		7	AW > AL	0.00								
		7	W > AW	0.04								

Trichoptera (Table 1b Cont.)

	Substrate effects				Effects of time (d)				Site effects			
gut content	site	day	comparison	p	site	substrate	comparison	p	day	substrate	comparison	p
Other Vege	N	7	AW > AL	0.00	SB	AW	d30 > d60	0.04	2	L, W, AW	N > SB	0.00, 0.00, 0.02
									7	W, AW	N > SB	0.00, 0.00
Animal					SB	AW	d7 > d2	0.00				
						AW	d30 > d7	0.01				
Diatoms	SB	7	AW > W	0.05	SB	AW, L	d7 > d30	0.00, 0.01	7	L, AW	SB > N	0.01, 0.00

Table 2. Gut contents of invertebrates in terms of occurrence (% larvae with contents)

Taxa (time period)	Trt-site	FPOM[1]	Biofilm[2]	Fiber	Diatoms	Cotton-wood	Desmids	Animal	Other Vege.
Chironomidae	L-SB	*	32	16	44	6	4	< 1	0
(days 2-30)	AL-SB	*	31	14	61	2	3	0	0
	WS-B	*	60	10	62	4	4	0	0
	AW-SB	*	61	15	58	2	3	< 1	0
	L-N	*	65	34	2	8	0	2	0
	AL-N	*	93	25	6	3	0	2	0
	W-N	*	97	33	3	8	0	4	0
	AW-N	*	80	41	3	12	0	3	0
Chironomidae	L-SB	*	90	18	2	4	0	5	0
(day 60)	AL-SB	*	90	10	6	2	4	2	0
	WS-B	*	90	24	3	2	1	0	0
	AW-SB	*	90	31	13	4	2	0	0
Trichoptera	L-SB	*	43	30	8	8	4	21	3
(days 2-30)	AL-SB	*	26	24	20	0	6	6	4
	WS-B	*	66	29	8	7	4	17	8
	AW-SB	*	46	31	17	5	8	20	4
	L-N	*	78	56	0	5	0	14	25
	AL-N	*	94	61	0	0	0	17	39
	W-N	*	77	60	0	5	0	9	44
	AW-N	*	65	60	0	5	0	8	47
	seeds – LN (7), WN (16), AWN (2)								

Table 2 cont.

Trichoptera Cont.	Trt-site	FPOM[1]	Biofilm	Fiber	Diatoms	Cotton-Wood	Desmids	Animal	Other Vege.
(day 60)	[3]L-SB	*	0	0	0	0	0	0	0
	AL-SB	*	49	22	5	3	8	11	19
	WS-B	*	58	26	9	7	5	23	28
	AW-SB	*	30	15	0	3	0	0	27
Subsamples:									
Ephemeroptera		*	79	11	0	8	0	0	0
Plecoptera		*	100	0	0	0	0	0	0
Oligochaeta		*	100	50	0	17	0	0	0
Zooplankton		*	89	0	5	0	0	0	0

[1]Essentially all larvae contained FPOM

[2]Chironomidae day 60 biofilm was estimated to be at least 90%

[3]L-SB = only two Trichoptera were collected from this treatment, both with very little FPOM.

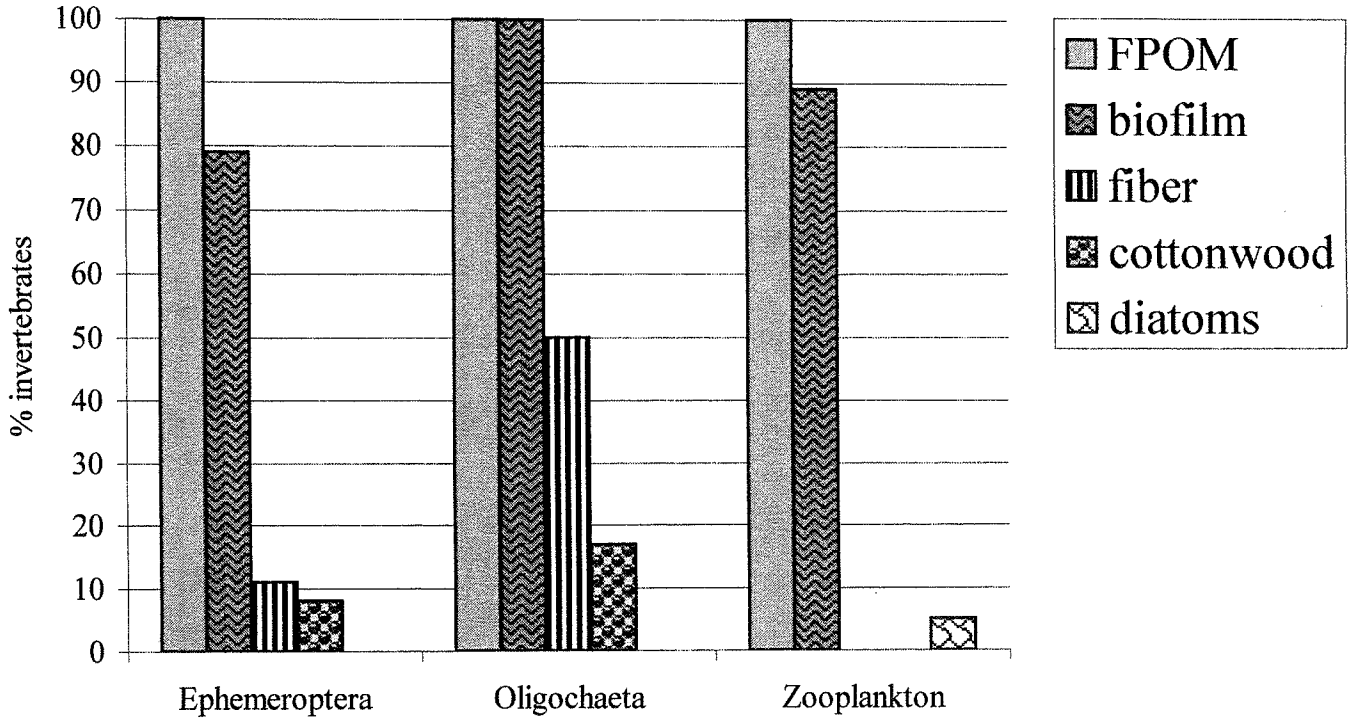


Figure 1. Subsamples analyzed to determine relative abundance (%) of Ephemeroptera, Oligochaeta, and zooplankton that contained specific gut contents on days 2-30.

2.6.6. Appendix E

Trophic Relationships

Table 1. Trophic relationships in terms of, maximum relative abundance (%) of A) invertebrates and B) invertebrate taxa, within functional feeding groups as described by Merritt and Cummins (1996); mean (±SD) of day 2-30 totals of the four substrate types within each site (SB & N). Individual taxa were placed in more than one FF group when appropriate. CG = collector-gatherer, CF = collector-filterer, SHH = shredder-herbivore, PRED = predator, SCR = scraper, PH = piercer-herbivore, SHD = shredder-detrivore.

A. Invertebrate Relative Abundance (%)

	CG	CF	SHH	PRED	SCR	PH	SHD
Total invertebrates							
SB	49(23)	24(8)	42(18)	30(15)	< 1(<1)	< 1(<1)	none
N	60(5)	19(5)	8(1)	27(7)	13(4)	< 1(<1)	< 1(<1)
*high values	W/AW-SB	L/AL-SB	W/AW-SB	AL-SB AL-N			
Invertebrates (excluding zooplankton)							
SB	87(4)	12(4)	75(2)	7(3)	<1(<1)	< 1(<1)	none
N	77(5)	20(5)	11(1)	10(2)	17(5)	< 1(<1)	< 1(<1)
Chironomidae							
SB	99(<1)	< 1(<1)	95(2)	< 1(<1)	< 1(<1)	none	none
N	77(10)	15(11)	17(3)	21(7)	4(3)	none	none
*high values	AL-N	W-N		W/AW-N			
Trichoptera							
SB	<1(<1)	97(1)	45(8)	44(8)	2(<1)	2(<1)	none
N	32(10)	67(10)	43(9)	13(3)	< 1(<1)	none	none
*high values	AL-N	W/L-N	AL-SB AL/AW-N	AL-SB			

B. Taxa Relative Abundance (%)

	CG	CF	SHH	PRED	SCR	PH	SHD
Chironomidae							
SB	86(5)	16(8)	29(8)	13(6)	6(4)	none	none
N	80(4)	22(8)	25(4)	35(12)	7(2)	none	none
*high values		W/L-SB, W/AW-N	W/AL-SB	L-N			
All other taxa							
SB	34(12)	37(9)	3(4)	33(7)	11(5)	8(4)	none
N	51(4)	31(2)	10(1)	28(4)	18(3)	1(2)	2(2)
*high values	AW-SB	L/AL-SB		W-SB			

* high values = Where large deviations in taxa number occur, substrates with the higher values are listed.

Table 2. Trophic relationships in terms of maximum abundance and relative abundance (%) of a) total invertebrates and b) data affected by the omission of zooplankton, within functional feeding groups as described by Merritt and Cummins (1996); includes substrates L, AL, W, and AW from days 2, 7, 30, and 60 sites SB and N, and mean (±SD) of days 2-30. CG = collector-gatherer, CF = collector-filterer, SHH = shredder-herbivore, PRED = predator, SCR = scraper, PH = piercer-herbivore, SHD = shredder-detrivore.

a) total invertebrates – site N; abundance and (relative abundance; %)

Trt	Day	N	CF	CG	CG/ CF	CG/ SHH	CF/ SHH/ PRED	CG/ SHH/ PRED	PRED	CG/ SCR	CG/ PRED/ SCR	CG/ PRED	SHH	SCR/ PH/ PRED	SHD/ CG	Other
LN	2	123	37	36	1	5	6	-	21	8	-	9	-	-	-	-
LN	7	171	9	82	1	10	-	7	44	15	-	2	-	1	-	-
LN	30	39	6	22	-	-	-	2	8	1	-	-	-	-	-	-
LN	2-30	333	52	140	2	15	6	9	73	24	-	11	-	1	-	-
(%)	2-30		(16)	(42)	(<1)	(5)	(2)	(3)	(22)	(7)		(3)		(<1)		
ALN	2	94	19	20	-	6	1	-	35	11	-	-	-	-	2	-
ALN	7	365	24	114	2	19	4	5	136	48	-	11	2	-	-	-
ALN	30	57	17	25	-	-	-	-	9	4	-	2	-	-	-	-
ALN	2-30	516	60	159	2	25	5	5	180	63	-	13	2	-	2	-
(%)	2-30		(12)	(31)	(<1)	(5)	(1)	(1)	(35)	(12)		(3)	(<1)		(<1)	
WN	2	220	71	36	4	9	8	4	42	32	1	13	-	-	-	-
WN	7	434	61	118	2	21	4	7	111	73	2	28	5	-	-	1 cf/scr
WN	30	460	99	214	-	16	-	7	46	74	-	3	-	-	-	1 cf/cg/shh
WN	2-30	1114	231	368	6	46	12	18	199	179	3	44	5	-	-	2
(%)	2-30		(21)	(33)	(<1)	(4)	(1)	(2)	(18)	(16)	(<1)	(4)	(<1)			(<1)
AWN	2	209	41	63	4	10	6	2	47	28	-	4	-	1	-	3 cf/cg/shh
AWN	7	134	12	54	1	10	2	1	18	30	-	4	2	-	-	-
AWN	30	33	1	24	-	-	-	-	4	-	-	3	-	-	1	-
AWN	2-30	376	54	141	5	20	8	3	69	58	-	11	2	1	1	3
(%)	2-30		(14)	(38)	(1)	(5)	(2)	(1)	(18)	(15)		(3)	(<1)	(<1)	(<1)	(1)

Table 2a cont. (total invertebrates) – Site SB; abundance and (relative abundance, %)

Trt	Day	N	CF	CG	CG/ CF	CG/SHH	CF/SHH/ PRED	CG/SHH/ PRED	PRED	CG/ SCR	CG/ PRED	SCR/PH	SCR/PH/ PRED
LSB	2	98	20	3	2	58	5	-	8	-	2	-	-
LSB	7	502	64	42	-	344	28	-	15	1	6	2	-
LSB	30	1372	417	54	-	103	13	-	785	-	-	-	-
LSB	2-30	1972	501	99	2	505	46	-	808	1	8	2	-
(%)	2-30		(25)	(5)	(<1)	(26)	(2)		(41)	(<1)	(<1)	(<1)	
LSB	60	226	60	14	-	102	2	-	48	-	-	-	-
ALSB	2	77	15	6	-	45	-	-	9	-	2	-	-
ALSB	7	412	57	55	-	203	38	1	55	1	1	1	-
ALSB	30	801	323	10	-	26	-	-	442	-	-		-
ALSB	2-30	1290	395	71	-	274	38	1	506	1	3	1	-
(%)	2-30		(31)	(6)		(21)	(3)	(<1)	(39)	(<1)	(<1)	(<1)	
ALSB	60	375	97	82	1	165	12	-	9	-	2	7	-
WSB	2	263	37	6	-	196	9	-	14	-	-	-	-
WSB	7	2238	114	461	1	1548	53	1	42	7	6	4	-
WSB	30	1022	311	65	3	203	19	-	414	3	1	1	2
WSB	2-30	3523	462	532	4	1947	81	1	470	10	7	5	2
(%)	2-30		(13)	(15)	(<1)	(55)	(2)	(<1)	(13)	(<1)	(<1)	(<1)	(<1)
WSB	60	1167	253	141	10	694	5	-	45	3	-	16	-
AWSB	2	276	49	5	-	175	10	-	36	1	-	-	-
AWSB	7	1426	123	189	-	1019	51	-	38	1	3	2	-
AWSB	30	1345	296	131	1	455	20	-	433	2	3	4	-
AWSB	2-30	3047	468	325	1	1649	81	-	507	4	6	6	-
(%)	2-30		(15)	(11)	(<1)	(54)	(3)		(17)	(<1)	(<1)	(<1)	
AWSB	60	1237	184	258	17	699	16	1	58	-	2	2	-

Table 2 cont.

b) Invertebrates with zooplankton omitted; included are data only that were affected by the omission of zooplankton, see Table 2 (a) for the remaining data.

Trt	Day	N	CF	CG	CG/ CF	CG/ SHH	CF/ SHH/ PRED	PRED	CG/ SCR	CG/ PRED
LN	2	100	31					5		
LN	7	134	4	35				12		
LN	30	28	2					1		
LN & (%)	2-30	262	37 (14)	139 (53)		(6)		18 (7)	(9)	(4)
ALN	2	57	15	17				5		
ALN	7	226	14	111				10		
ALN	30	42	12	24				0		
ALN & (%)	2-30	325	41 (13)	152 (47)		(8)		15 (5)	(19)	(4)
WN	2	178	66					5		
WN	7	329	57	112				16		
WN	30	404	90	210				3		
WN & (%)	2-30	911	213 (23)	358 (39)		(5)	(1)	24 (3)	(20)	(5)
AWN	2	163	34					8		
AWN	7	115	11	49				5		
AWN	30	32						3		
AWN & (%)	2-30	310	46 (15)	136 (44)	(2)	(6)	(3)	16 (5)	(19)	(4)

Table 2b cont. (Site SB); abundance and (relative abundance, %)

Trt	Day	N	CF	CG	CG/SHH	CF/SHH/ PRED	PRED	CG/PRED
LSB	2	81	9				2	
LSB	7	467	44				0	
LSB	30	183	9				4	
LSB & (%)	2-30	731	62 (8)	(14)	(69)	(6)	6 (1)	(1)
LSB & (%)	60	120	0	(12)	(85)	(2)	2 (2)	
ALSB	2	61	8				0	
ALSB	7	325	22				3	
ALSB	30	37	1				0	
ALSB & (%)	2-30	423	31 (7)	(17)	(65)	(9)	3 (<1)	
ALSB & (%)	60	310	39 (13)	(26)	(53)	(4)	2 (3)	
WSB	2	233	10				1	
WSB	7	2184	81				21	
WSB	30	326	26				3	
WSB & (%)	2-30	2743	127 (5)	(19)	(71)	(3)	25 (1)	
WSB & (%)	60	1125	227 (20)		(62)		29 (3)	
AWSB	2	208	17				0	
AWSB	7	1353	83				5	
AWSB	30	654	19				19	
AWSB & (%)	2-30	2215	119 (5)	(15)	(74)	(4)	24 (1)	
AWSB & (%)	60	1153	117 (10)	(22)	(61)		41 (4)	

Table 3. Trophic relationships in terms of maximum relative abundance (%) of a) total invertebrates and b) data affected by the omission of zooplankton, within functional feeding groups, as described by Merritt and Cummins (1996), substrates L, AL, W, and AW within sites SB and N on days 2, 7, 30, and 60. Individual taxa were placed in more than one FF group when appropriate. CG = collector-gatherer, CF = collector-filterer, SHH = shredder-herbivore, PRED = predator, SCR = scraper, PH = piercer-herbivore, SHD = shredder-detrivore.

a) abundance and (relative abundance; %)

Trt site & Day	N	CG	CF	SHH	PRED	SCR	PH
L SB 2	98	65 (66)	27 (28)	63 (64)	15 (15)	-	-
L SB 7	502	393 (78)	92 (18)	372 (74)	49 (10)	3 (<1)	2 (<1)
L SB 30	1372	157 (11)	430 (31)	116 (8)	798 (58)	-	-
L SB 2-30	1972	615 (31)	549 (28)	551 (28)	862 (44)	3 (<1)	2 (<1)
L SB 60	226	116 (51)	62 (27)	104 (46)	50 (22)	-	-
AL SB 2	77	53 (69)	15 (19)	45 (58)	11 (14)	-	-
AL SB 7	412	261 (63)	95 (23)	242 (59)	95 (23)	2 (<1)	1 (<1)
AL SB 30	801	36 (4)	323 (40)	26 (3)	442 (55)	-	-
AL SB 2-30	1290	350 (27)	433 (34)	313 (24)	548 (42)	2 (<1)	1 (<1)
AL SB 60	375	250 (67)	110 (29)	177 (47)	23 (6)	7 (2)	-
W SB 2	263	202 (77)	46 (17)	206 (78)	24 (9)	-	1 (<1)
W SB 7	2238	2024 (90)	168 (8)	1603 (72)	103 (5)	11 (<1)	5 (<1)
W SB 30	1022	275 (27)	333 (33)	222 (22)	436 (43)	6 (<1)	3 (<1)
W SB 2-30	3523	2501 (71)	547 (16)	2031 (58)	563 (16)	17 (<1)	9 (<1)
W SB 60	1167	848 (73)	268 (23)	699 (60)	50 (4)	19 (2)	16 (1)
AW SB 2	276	181 (66)	59 (21)	185 (67)	46 (17)	1 (<1)	-
AW SB 7	1426	1212 (85)	174 (12)	1070 (75)	92 (6)	3 (<1)	2 (<1)
AW SB 30	1345	592 (44)	317 (24)	475 (35)	456 (34)	6 (<1)	4 (<1)
AW SB 2-30	3047	1985 (65)	550 (18)	1730 (57)	594 (19)	10 (<1)	6 (<1)
AW SB 60	1237	977 (79)	200 (16)	716 (58)	77 (6)	2 (<1)	2 (<1)

Table 3a cont.; abundance and (relative abundance, %)

Trt site & Day	N	CG	CF	SHH	PRED	SCR	PH	SHD
L N 2	123	59 (48)	44 (36)	11 (9)	36 (29)	8 (7)	-	-
L N 7	171	117 (68)	10 (6)	17 (10)	54 (32)	16 (9)	1 (<1)	-
L N 30	39	25 (64)	6 (15)	2 (5)	10 (26)	1 (3)	-	-
L N 2-30	333	201 (60)	60 (18)	30 (9)	100 (30)	25 (8)	1 (<1)	-
AL N 2	94	39 (41)	20 (21)	7 (7)	36 (38)	11 (12)	-	2 (2)
AL N 7	365	199 (55)	30 (8)	30 (8)	156 (43)	48 (13)	-	-
AL N 30	57	31 (54)	17 (30)	-	11 (19)	4 (7)	-	-
AL N 2-30	516	269 (52)	67 (13)	37 (7)	203 (39)	63 (12)	-	2 (<1)
W N 2	220	99 (45)	83 (38)	21 (10)	68 (31)	33 (15)	-	-
W N 7	434	251 (58)	68 (16)	37 (9)	152 (35)	76 (18)	-	-
W N 30	460	315 (68)	100 (22)	24 (5)	56 (12)	74 (16)	-	-
W N 2-30	1114	665 (60)	251 (23)	82 (7)	276 (25)	182 (16)	-	-
AW N 2	209	114 (55)	54 (26)	21 (10)	60 (29)	29 (14)	1 (<1)	-
AW N 7	134	100 (75)	15 (11)	15 (11)	25 (19)	30 (22)	-	-
AW N 30	33	28 (88)	1 (3)	-	7 (21)	-	-	1 (3)
AW N 2-30	376	242 (64)	70 (19)	36 (10)	92 (24)	59 (16)	1 (<1)	1(<1)

Table 3 cont.

b) Invertebrates with zooplankton omitted; included are data only that were affected by the omission of zooplankton, see Table 3a for the remaining data; abundance and (relative abundance, %).

Trt site & Day	N	CG	CF	SHH	PRED	SCR	Trt site & Day	N	CG	CF	SHH	PRED	SCR
L SB 2	81	(80)	16 (20)	(78)	9 (11)		L N 2	100	58 (58)	38 (38)	(11)	20 (20)	(8)
L SB 7	467	(84)	72 (15)	(80)	34 (7)		L N 7	157	(75)	5 (3)	(11)	22 (14)	(10)
L SB 30	183	(86)	22 (12)	(63)	17 (9)		L N 30	28	(89)	2 (7)	(7)	3 (11)	(4)
L SB 2-30	731	(84)	110 (15)	(75)	60 (8)		L N 2-30	262	200 (76)	45 (17)	(11)	45 (17)	(8)
L SB 60	120	(97)	2 (2)	(87)	4 (3)								
AL SB 2	61	(87)	8 (13)	(74)	2 (3)		AL N 2	57	36 (63)	16 (28)	(12)	6 (11)	(19)
AL SB 7	325	(80)	60 (18)	(74)	43 (13)		AL N 7	226	196 (87)	20 (9)	(13)	30 (13)	(21)
AL SB 30	37	(97)	1 (3)	(70)	0		AL N 30	42	30 (71)	12 (29)		2 (5)	(10)
AL SB 2-30	423	(83)	69 (16)	(74)	45 (11)		AL N 2-30	325	269 (83)	48 (15)	(11)	38 (12)	(19)
AL SB 60	310	(81)	52 (17)	(57)	16 (5)								
W SB 2	233	(87)	29 (12)	(88)	11 (5)		W N 2	178	(56)	78 (44)	(12)	31 (17)	(19)
W SB 7	2184	(93)	135 (6)	(73)	82 (4)		W N 7	329	245 (74)	64 (19)	(11)	57 (17)	(23)
W SB 30	326	(84)	48 (15)	(68)	25 (8)	(2)	W N 30	404	311 (77)	91 (23)	(6)	13 (3)	(18)
W SB 2-30	2743	(91)	212 (8)	(74)	118 (4)		W N 2-30	911	655 (72)	233 (26)	(9)	101	(20)
W SB 60	1125	(75)	242 (22)	(62)	34 (3)							(11)	
AW SB 2	208	(87)	27 (13)	(89)	10 (5)		AW N 2	163	(70)	47 (29)	(13)	21 (13)	(18)
AW SB 7	1353	(90)	134 (10)	(79)	59 (4)		AW N 7	115	95 (83)	14 (12)	(13)	12 (10)	(26)
AW SB 30	654	(91)	40 (6)	(73)	42 (6)		AW N 30	32				6 (19)	
AW SB 2-30	2215	(90)	201 (9)	(78)	111 (5)		AW N 2-30	310	237(76)	62 (60)	(12)	39 (13)	(19)
AW SB 60	1153	(85)	133 (12)	(62)	60 (5)								

Table 4. Relative abundance (%) of Zooplankton (Zoo), Chironomidae (Chiron), and Trichoptera (Trich) in Functional Feeding Groups for leaf packs (L), artificial leaf packs (AL), wood (W), and artificial wood (AW) at a) sites SB (upstream) and N (downstream); combined data from days 2-30, and b) site SB d60.

a) days 2-30 combined; relative abundance (%)

Taxa	Trt-site	N	CG	CF	SHH	PRED	SCR	PH	Trt site	N	CG	CF	SHH	PRED	SCR
Zoo	L-SB	1241	-	35	-	65	-	-	L-N	71	1	21	-	78	-
	AL-SB	867	-	42	-	58	-	-	AL-N	191	4	10	-	86	-
	W-SB	780	-	43	-	57	-	-	W-N	203	5	9	-	86	-
	AW-SB	832	-	42	-	58	-	-	AW-N	66	8	12	-	80	-
Chiron	L-SB	530	99	1	95	<1	<1	-	L-N	76	80	7	17	29	4
	AL-SB	297	99	1	93	1	0	-	AL-N	83	88	6	18	14	2
	W-SB	2008	100	<1	97	<1	1	-	W-N	139	64	30	19	24	7
	AW-SB	1689	100	<1	97	<1	<1	-	AW-N	79	77	19	13	16	1
Trich	L-SB		0	98	44	44	2	2	L-N		26	74	41	15	0
	AL-SB		0	99	56	56	1	1	AL-N		47	52	50	12	0
	W-SB		<1	97	39	38	2	2	W-N		25	75	30	8	1
	AW-SB		1	96	40	39	3	3	AW-N		31	65	50	15	0

b) site SB d60 (Table 4 cont.); relative abundance (%)

Taxa	Trt-site	N	CG	CF	SHH	PRED	SCR	PH
Zoo	L-SB	106	-	57	-	43	-	-
	AL-SB	65	-	89	-	11	-	-
	W-SB	42	-	62	-	38	-	-
	AW-SB	84	-	80	-	20	-	-
Chiron	L-SB	103	100	0	99	-	-	-
	AL-SB	174	100	< 1	95	1	-	-
	W-SB	709	99	2	98	-	-	-
	AW-SB	724	100	2	97	<1	-	-
Trich	L-SB	2	-	100	100	100	-	-
	AL-SB	55	-	87	22	22	13	13
	W-SB	230	-	93	2	2	7	7
	AW-SB	129	-	98	12	12	2	2