UNIVERSITY OF WISCONSIN-LA CROSSE

Graduate Studies

INFLUENCE OF MACROPHYTE ABUNDANCE ON POPULATION DYNAMICS OF SLIMY SCULPIN (*COTTUS COGNATUS*) AND RELATED FOOD WEB STRUCTURE IN COLD-WATER STREAMS IN WESTERN WISCONSIN

A Manuscript Style Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of Master of Science in Biology

Jenna L. Merry

College of Science and Health
Aquatic Science

May, 2015

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By Jenna L. Merry

We recommend acceptance of this thesis in partial fulfillment of the candidate's requirements for the degree of Master of Science in Biology-Aquatic Science.

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ABSTRACT

Merry, J. L. Influence of macrophyte abundance on population dynamics of slimy sculpin (*Cottus cognatus*) and related food web structure in cold-water streams in western Wisconsin. MS in Biology-Aquatic Science, May 2015, 56pp. (E. Strauss)

Slimy sculpin (*Cottus cognatus*) are important inhabits of cold-water streams in southwestern Wisconsin. Unpublished data suggests that small-bodied sculpin are more abundant in stream riffles with high macrophyte cover than those where macrophytes are scarce. The objectives were to determine if the presence of abundant macrophytes affects the density of different size classes of sculpin and those differences were driven by the influence of macrophyte presence of local food web structure. Basal carbon sources, macroinvertebrate prey, and slimy sculpin were sampled during the fall in the Coon Creek watershed of Wisconsin, and food webs were constructed using stable isotope analysis. Data were compared between sites with high and low macrophyte abundance. Periphyton biomass and the density and biomass of common macroinvertebrate families were similar between areas of high and low macrophyte abundance. Slimy sculpin were not segregated by size between these site types, however the total density of slimy sculpin was significantly higher in areas with high macrophyte abundance. Macrophyte abundance influences sculpin distribution by providing refuge from predators and providing greater prey availability. The food webs at sites with abundant and scarce macrophyte cover were detritus based. In the fall, aquatic and terrestrial based detritus are important carbon sources in areas with high-macrophyte growth.

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INTRODUCTION

Inland waters are perhaps some of the most sought after resources on the planet because of the various ecological services they provide (Williams 2002). The study of inland freshwaters is critical to keeping these systems healthy and functioning. Though large rivers and lakes are the most obvious contributors to the ecosystem services that humans use every day, these services would not be possible without the maintenance and healthy functioning of the smaller streams and tributaries that flow into them. In their own right, streams benefit humans by directly influencing the quality of water and the flow of nutrients available to larger water bodies, as well as maintaining habitats and food sources for various types of organisms (Meyer *et al.* 2003); most notably in western Wisconsin are the cold-water stream sport fish like trout.

In order to sustain valuable stream services, an understanding of the connections and interdependencies between the various groups of biota is essential. Not only do organisms interact on a whole-stream scale, but also on smaller scales, such as within pools, riffles, or macrophyte beds. Large- and small-scale interactions, such as predator-prey relationships, allow energy to flow through an ecosystem. The flow of energy through succeeding trophic levels can be mapped and analyzed through the construction of ecosystem food webs (Chapin III *et al.* 2011). Many consumers eat more than one type of prey item, so constructing accurate and proportional food webs can be complex. In the past, food webs have been constructed using gut content analysis and feeding observation, both of which become difficult as the size of food web organisms decrease.

More recently, the ability to map food webs more thoroughly has become easier with the introduction of stable isotope techniques (Fry and Sherr 1984, Estep and Vigg 1985; Fry 1988; Ehleringer and Rundel 1989; Hilderbrand et al. 1999; Kelly 2000; Post, 2002; Gorokhova *et al.* 2005; West et al. 2006; Schmidt *et al.* 2007; Symes and Woodborne 2009).

In the mid-1990s, ecologists began using stable isotopes to evaluate food web interactions in ecosystems. Stable isotopes can trace the sources and flow of energy and nutrients in a system if the sources have distinct isotopic signatures and if the isotopic signatures change in a predictable fashion as the material moves through food webs. Isotopes in the tissues of animals can aid in determining trophic status and food web position. Most elements occur naturally in several isotopic forms. Stable isotopes are unique because they do not diminish through radioactive decay. In an ecological and physiological context, stable isotopes of the same element are virtually identical to each other except that they have slightly different atomic masses (Peterson and Fry 1987). Also, in general, the "lighter" stable isotope is much more abundant than the "heavier" stable isotope (Clark and Fritz 1997).

There are many naturally occurring isotopes for various elements, but only a few are of practical to use in ecological studies. Hydrogen (H), carbon (C), nitrogen (N), oxygen (O) and sulfur (S) are abundant elements and their isotopes represent some of the environmental isotopes. Environmental isotopes comprise a group of elements that are profuse in biological systems, as well as hydrological and geological systems. In food web analysis, the two most commonly used isotopes are those for nitrogen and carbon. These are used because they are present in macromolecules and are transferred through heterotrophy. The stable isotopes of these elements serve as tracers of nutrient and energy pathways (Clark and Fritz 1997).

All organisms contain a certain ratio of heavy to light stable isotopes for a given element, which is largely determined by an individual's diet (Schindler and Lubekin 2004). Fractionation is a change in this isotopic ratio in an organism relative to its resources. Although heavy and light isotopes are chemically similar, the light isotopes are processed easier during biological reactions because they have lower bond strengths. Physiological processes like respiration and excretion preferentially use and release lighter isotopes more readily than heavy isotopes. This leaves the tissues of the organism more enriched in the heavy isotope than their food source (Schindler and Lubekin 2004). There is some variation in the amount of carbon and nitrogen fractionation that occurs with the transfer of nutrients from prey to consumers (McCutchan *et al.* 2003). However, most consumers show a consistent enrichment in the heavy isotope compared with their food; this is known as trophic level shift. Producers, on the other hand become enriched in the lighter isotope because they preferentially take up the lighter isotope from their surroundings (Stuiver 1978). Plants utilizing the C4 metabolic pathway have more positive $\delta^{13}C$ composition in the range of -8 to -18‰ compared to other plants, -20 to -30‰, and algae, -12 to -23‰ (Smith and Epstein, 1971; O'Leary 1981; Deleens *et al.* 1983). Carbon isotope fractionation associated with algae can be quite small (~5 ppt) (Fogel and Cifuentes 1993). Stable isotope ratios for nitrogen and carbon, determined using isotope ratio mass spectrometry (IRMS), can be used to determine both the source of the organic material and the number of trophic levels in the food web (Post 2002). By plotting stable isotope ratios for ^{13}C and ^{15}N, the level at which an animal feeds at in a food web can be determined. Laboratory and field studies demonstrate predictable increases in $\delta^{15}N$ (between 2 to 3‰) and $\delta^{13}C$ (between 0-1‰) between consumers and their diet, i.e. between trophic levels (Peterson and Fry 1987).

Diagraming ecosystem food webs allows researchers to provide policy-makers with ecosystem-encompassing data, which allows the latter to draft more effective environmental legislation about issues like fisheries management and farming practices (Rounick and Winterbourn 1986). The conservation of services provided by streams, like vigorous sport fish populations, depends on the maintenance of healthy populations of organisms in lower trophic levels. Maintaining the health of biota from several interacting trophic levels can be complex. Therefore, the application of stable isotope technique to understand food webs is an important step in protecting the integrity of ecosystems and the valuable services they provide to the public.

Streams, as a whole, are important to study because of the services they provide to humans and other organisms. However, examining the smaller components and processes that make up a stream is equally important. Macrophytes are important to stream ecosystems in general. For example, they provide structural integrity to the sediments (Stephens *et al.* 1963) as well as habitat for freshwater invertebrates and various microorganisms (Iversen *et al.* 1985). Submerged macrophyte biomass can reach extremely high levels during the growing season in streams and evidence is mounting that they do play a significant role in various aspects of stream dynamics (Clarke 2002).

The most obvious effects that macrophytes have are on the physical dynamics of a stream, especially in regards to flow velocity and sedimentation. Their presence can greatly reduce water velocity within the beds, at their margins, and immediately downstream. The extent to which aquatic macrophytes reduce or alter water velocity is dependent upon plant morphology and bed structure, but in general plants have high frictional force and act as physical barriers to water flow. As macrophyte beds grow larger, they can divert the main flow or thalweg of the channel to areas that are less vegetated, thus also having an influence on channel shape by increasing sinuosity (Clark 2002).

Flow velocity can have influences on sedimentation rates. In areas where macrophytes are abundant and decrease flow velocity, there is a subsequent increase in the deposition of sediments and organic matter because macrophytes directly trap material or decrease water velocity to the point where suspended solids fall out of the water column. Therefore, substrates in macrophyte beds tend to be finer than those between beds. (Gregg and Rose 1982; Sand-Jensen 1998). As sediment and other particulate matter settle out of the water, turbidity decreases and light attenuation increases. However, this sediment also fills in spaces between cobbles and can bury macrophytes, which acts to decrease benthic habitat by increasing embeddedness.

Not only do macrophytes retain sediment, but also organic matter and nutrients, and therefore affect chemical cycles in streams. Nutrient cycles in lotic or flowing systems are very similar to those in lentic systems. They have biotic and abiotic compartments and nutrients are converted to different forms between and within these compartments. However, in lotic systems these cycles work in conjunction with downstream transport, producing cycles that are spiral shaped and move downstream. Submerged macrophytes act as retentive elements that slow the downstream spiraling of nutrients, especially nitrogen and carbon. They do this in a number of ways. Firstly, they can block and trap coarse organic material from flowing downstream (Wharton *et al.* 2006; Koetsier and McArthur, 2000). Therefore the decomposition of those particles occurs within the macrophyte beds and more nutrients will be available to localized flora and fauna. Secondly, nutrients that are assimilated by these plants are largely retained until senescence occurs in the fall/winter. Consequently, these elements remain in the biotic compartment longer than in areas with few macrophytes (Riis *et al.* 2012).

The increased nutrient retention decreases the availability of those nutrients to organisms downstream of macrophyte beds and increase nutrient availability to local organisms when diebacks occur. The effects that macrophytes have on the physical and chemical nature of streams, directly influences the other aquatic biota. Macrophytes add structure to the streambed and provide large habitable areas that can be colonized by epiphytes and invertebrates. Lastly, macrophytes also provide refuge from predators and spawning or foraging habitat for a variety of small bodied and juvenile fish species (Riis *et al.* 2012).

Despite increasing knowledge of the importance of submerged macrophytes on stream dynamics, the specific importance that macrophytes may have in relation to freshwater sculpin has not been extensively studied. Freshwater sculpin (*Cottus* spp.) comprise a group of small benthic fish that are found in both lentic and lotic habitats in North America, Eurasia, and Japan (Kinzinger *et al.* 2005). Of the four species of sculpin in Wisconsin, slimy sculpin (*C. cognatus*) and mottled sculpin (*C. bairdii*) are two common species of insectivorous sculpin native to southwestern streams (Becker 1983). *Cottus cognatus* has the widest distribution of all cottid species in North America (McDonald *et al.* 1982; Morrow 1974; Scott and Crossman 1979) ranging as far north as northern Quebec, Canada, south to Georgia, west to Oregon, and east to Virginia (Becker 1983). In Wisconsin, mottled and slimy sculpin are typically found in cool-water, rocky habitats of headwater streams that range from 0.5 to 3.0 m wide and at depths of 0.1 to 0.5 m. Recently, research investigating the use of sculpin as bioindicators has increased because some species are very sensitive to certain pollutants (Adams and Schmetterling 2007; Maret and MacCoy 2002) and sculpin tend to remain in a relatively small spatial area for most of their lives (Fisher and Kummer 2000; Gray *et al.* 2004; Yeardley 2000). Also, the nests of *C. cognatus* in particular may be sensitive to changes in stream characteristics such as flow regime, sedimentation (Keeler and Cunjak 2007), temperature, and streambed stability (Edwards and Cujak 2007).

In trout streams, sculpin can have dynamic relationships with multiple salmonid species (e.g., brown trout, *Salmo trutta,* and brook trout, *Salvelinus fontinalis*). These small fish serve as forage for large salmonids and may be a particularly important link between trout and lower trophic levels, most notably in large lake habitats (Van Oosten and Deason 1938). Not only are sculpin forage food for large brown trout (Becker 1983) and brook trout (Scott and Crossman 1979), they also compete with young trout for invertebrate prey (Ruetz *et al.* 2003; Zimmerman and Vondracek 2006). It has been suggested that sculpin may also feed on the eggs of these salmonids (Clary 1972; Ward *et al.* 2008), but whether or not this behavior restricts trout populations is unclear. Several studies have reported that egg predation may occur only under specific conditions or on rare occasions (Greeley 1932; Koster 1937; Moyle 1977).

Although the ways that sculpin may affect trout populations remain unclear, studies have shown than sculpin can have significant influences on macroinvertebrate communities. Cuker *et al.* (1992) found that sculpin predation on Trichoptera larvae and Chironomidae larvae reduced those populations by 50% and 27%, respectively. Mundahl *et al.* (2012a) showed that slimy sculpin in trout streams in southeastern Minnesota showed strong preference for Diptera larvae and Amphipoda, but perhaps because these items were abundant in the study streams. Cheever and Simon (2009) reported that the effects of sculpin predation on benthic invertebrate assemblages were seasonal. In their study, sculpin were able to suppress the abundance of grazing invertebrates in the spring season, but the cause of this seasonality was unclear. Not only can sculpin have temporal effects on invertebrate assemblages, their diet also shifts with age (Petrosky and Waters 1975). In a study conducted by Petrosky and Waters (1975) in Valley Creek in Minnesota, *Gammarus* sp. was the most important food for sculpin in that stream. *Gammarus* predation increased with fish age, as did predation on Trichoptera and Gastropoda, while Dipteran predation decreased. Petty and Grossman (1996 and 2010) suggest that invertebrate prey abundance is the dominant factor in patch choice for mottled sculpin. Home ranges and growth of sculpin may also be influenced by the density of adult sculpin, intraspecific competition, and stream flow (Petty and Grossman 2004 and 2007). Mundahl *et al.* (2012b) showed that preferred habitat characteristics were different between juvenile and adult slimy sculpin in cold-water Mississippi River tributaries, which further alludes to a link between habitat choice and food preference or availability. In their study, young-of-the-year sculpin selected for smaller substrates like gravel whereas adults tended to select for boulders and rubble. Both groups appeared to select for vegetated areas as well, but this was done so by a higher percentage of young of the year sculpin. However, this may have been due to the availability of habitat type because when the data were normalized for availability, selection of vegetation by young of the year and adult sculpin were more even.

Unpublished data suggest that in the cold-water streams of western Wisconsin, a larger percentage of juvenile and small-bodied sculpin are found in macrophyte beds when compared to larger, adult sculpin (Laukkanen 2012), which corresponds with the data published by Mundahl *et al.* (2012b). A difference in diet between juveniles and adults could related to this divergence. Juveniles may also be forced to occupy macrophytes due to intra-specific competition whereby larger sculpin out-compete juveniles for preferred, rocky substrate, or perhaps juveniles find shelter within macrophytes therefore increasing their chance of survival where predators are abundant. Chivers *et al.* (2001) showed that slimy sculpin display threat sensitive predator avoidance based largely on visual cues. The sculpin in their study showed a tendency to avoid cages with large trout, but not cages with small trout. Perhaps the young sculpin seek shelter in macrophytes when stimulated by a predator. Intraspecific competition could also contribute to the disparity as aggressive adults chase away smaller juveniles or out-compete them for preferred substrate. Majeski and Cochran (2009) found that spawning by slimy sculpin on rocks is highly dependent on the size of the rocks available in a habitat, coarse substrate being the preferred. When fish density is high and there is limited preferred habitat, some juvenile and small-bodied individuals may be forced to occupy less desirable substrates (Davey *et al.* 2005).

The objectives of this research were to determine whether the presence of abundant macrophytes affects the density of different size classes of sculpin present and whether the distribution differences were driven by the influence of macrophyte presence on local food web structure. Several hypotheses were formulated based on these objectives.

1. The most abundant macroinvertebrate groups will differ in biomass and density between sites with abundant macrophytes and sites with few macrophytes. Macrophytes provide more physical areas for invertebrates to inhabit (Becerra-Munoz and Schramm 2007; Grubaugh *et al.*, 1997). Their effects on stream dynamics, such as reducing water velocity, can make areas containing macrophytes more suitable for smaller organisms.

2. Small-bodied sculpin (<5 cm) are more abundant than large-bodied sculpin (>6 cm) in sites with dense macrophyte cover. This is hypothesized because macrophyte beds have the potential to provide small sculpin with shelter from predators and large sculpin out-compete small sculpin for preferred cobble-substrate habitat. Also, macrophyte beds support larger macroinvertebrate communities, which can support small sculpin that may not be able to compete for food in areas where invertebrates are not as abundant.

3. Sculpin in sites with macrophytes will contain a greater mass of food in their guts than sculpin of the same size in areas without macrophytes. Because macrophyte beds have the potential to support large invertebrate communities, food availability is expected to be greater in dense-macrophytes sites, therefore more macroinvertebrates would be available to each individual sculpin. A greater percentage of sculpin collected from macrophyte-abundant sites will have *Baetis* spp. in their guts than those collected from sites with low macrophyte abundance. Unpublished data indicate that sculpin select for mayfly nymphs (*Baetis* spp.), an invertebrate herbivore, at open-canopy sites in the Coon Creek watershed (Laukkanen 2012). As herbivores *Baetis* spp. feed on periphyton, which is likely in higher abundance at open-canopy sites where photosynthetic rates are high due to increased availability of sunlight (Behmer and Hawkins 1986; Richards and Minshall 1988). *Baetis* spp. is expected to be more abundant in these areas as well.

4. Food webs constructed with stable isotope analysis will show that *Gammarus pseudolimneus* is a larger component in sculpin diet at macrophyte-abundant sites than sites with low macrophyte abundance. *Gammarus* sp. are crustaceans that possess a completely aquatic life cycle. Therefore their abundance will not fluctuate as much as aquatic insects that experience seasonal adult emergence. This allows *Gammarus* sp. to be a consistent source of food to sculpin inhabiting vegetated areas of the stream, where *Gammarus* sp. are most abundant.

5. The food web structure of high-macrophyte sites will differ from the structure of food webs in sites with low macrophytes. Sculpin collected from macrophyte abundant sites will have higher isotopic signals for $\delta^{15}N$ and $\delta^{13}C$ relative to those collected from sites with few macrophytes (Hershey *et al.* 2006; Hicks 1997). If

the presence or absence of macrophytes has an effect on periphyton abundance, invertebrate community assemblage, and the distribution of sculpin, the overall effect will be to change the structure of the food web where macrophytes occur. Based on this assumption, the food web constructed for macrophyte-abundant sites is expected to show a predictable trophic shift between primary producers (e.g., periphyton and macrophytes), collecting, grazing, and shredding macroinvertebrates (e.g., Glossossomatidae, Baetidae, and Gammaridae), and sculpin. Conversely the food webs representing sites with low macrophyte abundance will show a more predictable trophic shift between allochthonous detritus, filter-feeding and shredding macroinvertebrates (e.g., Brachycentridae, Simuliidae, Gammaridae, Tipulidae), and sculpin.

METHODS

Study Area

Three second-order streams were examined during September and October 2012. Coon Creek, Spring Coulee Creek, and Rullands Coulee Creek are located in the Coon Creek watershed of Wisconsin, which covers portions of Monroe, Vernon, and La Crosse counties. Discharging into the Mississippi River near the town of Stoddard, Wisconsin, the Coon Creek watershed (196 km^2) makes up part of the unglaciated Driftless Area of the Midwestern United States (Cavanaugh *et al.* 2004). The watershed is comprised of various types of land use. Row crop agriculture and cattle grazing are prominent at blufftop elevations whereas deciduous forests make up much of the valley slopes. All three study streams have relatively stable temperatures and steady base flow because they arise from groundwater springs.

Two riffle sites from each of the three streams were chosen based on their physical characteristics, most notably the observable abundance of aquatic macrophytes contained at each (Figure 1). All sites covered a 20-meter stream reach. The pair of riffles in each stream included a downstream site with an open canopy and observably dense macrophyte cover, hereafter referred to as a high-macrophyte site, and an upstream site with dense riparian canopy and sparse or no macrophyte cover, hereafter referred to as a low-macrophyte site. Each reach was divided into eleven transects perpendicular to stream flow and two meters apart. The purpose of the study was to determine whether the presence of abundant macrophytes affects the density of different size classes of sculpin present and whether their presence also affect the structure of local food webs. Data collected from several trophic levels were compared between high- and low-macrophyte

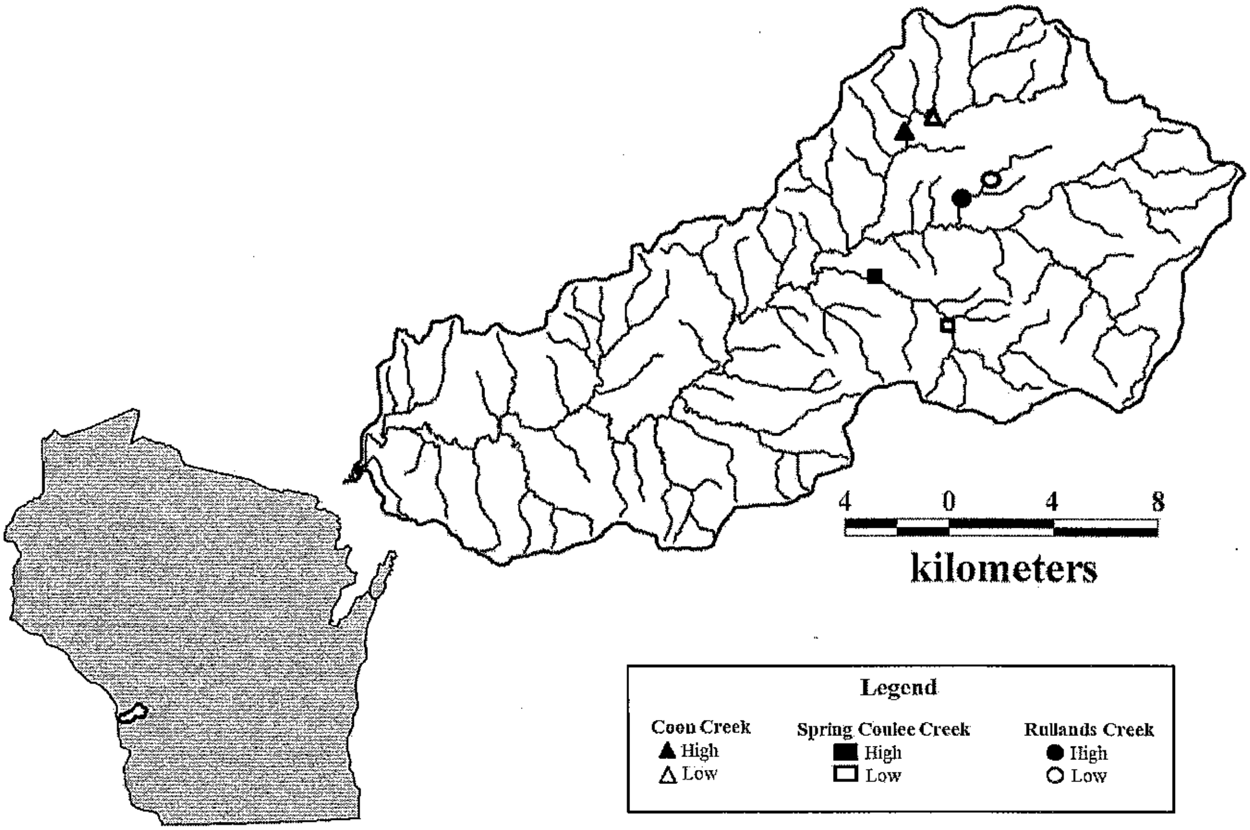

Figure 1. Study sites with high and low macrophyte abundance in three cold-water streams of the Coon Creek watershed in western Wisconsin.

Physical Habitat

The average flow velocity of each stream site was determined at 60% depth in the thalweg using a velocity meter (Marsh-McBirney Flow Meter ®2000, Marsh-McBirney, Frederick, MD) at eleven transects. Temperature, dissolved oxygen, conductivity, and pH data were collecting with a Hydrolab (DS5 Sonde) in the thalweg of each site. Discharge was measured with a salt slug release (Moore 2004; Moore 2005). The slug solution was released 300 meters upstream of the reach and concentration of rhodamine and salt were collected immediately downstream of the last transect with a Hydrolab (DS5 Sonde). The concentration curve was then used to calculate the average discharge within each stream reach. Canopy cover was estimated at each site as the mean of four individual readings at three points in the reach (upper, middle, and bottom) with a spherical densitometer (Forest Densiometers, Model-A, Rapid City, SD).

Substrate analysis was conducted in each reach using a gravelometer (Albert Scientific, West Trenton, NJ) and the substrate categorized according to a modified Wentworth scale (Wolman 1954).

Macrophytes

Percent cover of macrophytes in each reach was determined with a 0.25 m^2 quadrat, divided into 272 squares. Stream reaches were divided into eleven transects, 2 m apart. One quadrat was dropped, without bias, into the stream at each transect. Percent cover was estimated within the quadrat for each transect and the average (± standard deviation) of the quadrats was calculated for each site. The quadrats were used to calculate percent cover using the equation: $C\% = (N_p / 272) \times 100$ where N_p is the number of squares in each quadrat with macrophytes present. Once the squares within the quadrat were counted, all submerged and partially submerged macrophytes were removed from the quadrat to assess the standing biomass of vegetation in each reach. Vegetation was rinsed in stream water and immediately stored on ice and in the dark until returned to the lab. At the lab, macrophytes were sorted by species and dried to a constant dry weight at 70°C (Bowden *et al.* 2006). The mean mass of each species per transect was calculated for each site and individual species and total macrophyte standing biomass were calculated.

After biomass was calculated, three homogenized subsamples of each macrophyte species from the Coon Creek paired sites were ground into a fine powder. Approximately four milligrams of dried samples was transferred into tin capsules and sent to the Stable Isotope Mass Spectrometry Laboratory (SIMSL) at Kansas State University. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ with a ThermoFinnigan Delta Plus mass spectrometer.

Periphyton

Epilithic periphyton biomass was collected from the surface of three rocks in each of eleven transects per site. Periphyton biomass on the rocks was assessed on site by using a tubular sampler and methods described by Steinman *et al.* (2006). A tubular sampler consists of a Plexiglas tube with a neoprene gasket at the base. The gasket end of the tube was placed over a portion of the sampled substratum. The tube was of known circumference so that the sampling area could be calculated. A brush and syringe were used to remove periphyton from the rocks. Rocks were used to sample periphyton because the leaves of macrophytes are too small and irregularly shaped to accurately sample for epiphytic periphyton. After the slurry was collected, it was immediately placed in a cold, dark environment. Periphyton was filtered in the laboratory with pre-weighed Whatman®GF/F glass fiber filters (47 mm; Piscataway, NJ) and frozen in aluminum foil until analysis was completed. Filters containing periphyton were cut into three sections. Dry mass of periphyton was estimated from one portion, followed by ash-free dry mass in accordance with Steinman *et al.* (2006). The second portion of the filters was placed in a dark canister with a known volume of 90% buffered acetone for chlorophyll analysis. Samples were extracted for 24 h at 4°C in the dark. After this, 3 mL of extract was pipetted into a cuvette and optical density was recorded at 750 nm and 664 nm using a spectrophotometer (Varian Cary 50 Bio UV/Visible Spectrophotometer). Phaeophytin-corrected chlorophyll calculations were made in accordance with Wetzel and Likens (1991).

The third portion of the periphyton filters from the Coon Creek sites was placed in an aluminum tray and dried in an oven at 60°C. Once dry, portions of the filter were homogenized so that 4 mg of periphyton could be packaged into tin capsules. Five to eight capsules were prepared and analyzed using isotope ratio mass spectrometry (IRMS) by the SIMSL at Kansas State University. Values for $\delta^{13}C$ and $\delta^{15}N$ were attained.

Macroinvertebrates

The biomass and density of the macroinvertebrate community at each site was assessed using a Hess sampler with 500 μm mesh. Each stream reach was divided into five evenly-spaced transects and one Hess sample was collected at each transect. Once collected, macroinvertebrates were held overnight in clean stream water to clear their digestive tracks and kept in sealed containers until deceased. Subsequently, the samples were preserved in 70% ethanol until analysis was completed. Invertebrates were sorted to family, then counted and dried in aluminum tins at 60°C until a constant weight was achieved. The dry weight of each taxon was recorded so that the standing biomass could be estimated for each site. For the Coon Creek sites, sub-samples of the most common taxa were prepared for stable isotope analysis. Dried subsamples were ground to a fine powder and approximately 2 mg were weighed and sealed in tin capsules. Samples were comprised of several individuals representing a family in order to achieve the required mass for analysis. Up to three replicate samples were prepared for each taxon. Samples were analyzed using IRMS by the SIMSL at Kansas State University and values for $\delta^{13}C$ and $\delta 1^{5}N$ were attained.

Slimy Sculpin

Slimy sculpin were collected with a kicknet and measured for total length. Beginning at the downstream end of each reach, a kicknet was placed perpendicular to the stream current. An area of approximately 0.5 m^2 was disturbed directly above the net which caused the sculpin to be swept into the kicknet screen by the current. The entire stream width and site length was sampled and the density for each reach was calculated. The collected sculpin were placed into an aerated bucket of stream water and measured (total length, nearest mm). The first 10 individual measuring < 5 cm and the first 10 individuals measuring > 6 cm were euthanized with an overdose of tricaine methanesulfonate (MS-222, Argent Chemical Laboratories, Inc., Redmond, WA) in accordance with Ross and Ross (2008). The euthanized individuals were kept in water, on ice until returned to the lab, where gut contents were collected by gastric lavage (Gelwick and Matthews 2006). Gut contents were made up of whole and partial organisms as well as fine particulates; therefore, contents were filtered through Whatman®GF/F glass fiber filters (47 mm; Piscataway, NJ). Whole and partial macroinvertebrates in the stomach contents were identified to family and Ivlev's Electivity Index (Ivlev 1961) was used to determine potential sculpin preferences for invertebrate prey. After gut contents were collected, a sample of epaxial muscle tissue was removed from each fish euthanized from the Coon Creek sites (Arrington and Winemiller 2002). For small sculpin, small fragments of bone may have remained in the muscle sample due to the difficulty of separating muscle from bone in such small body sizes. Muscle samples were dried in an oven at 60°C until a constant weight was achieved. Then approximately 1.5 milligrams of each of the twenty sculpin per site was weighed and sealed in tin capsules. Capsules were sent to the SIMSL at Kansas State University and for stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$.

Data Analysis

Paired t-tests were used to compare data between high- and low-macrophyte sites in each stream. Analysis for macrophyte samples included a comparison of percent cover, biomass, and diversity. Periphyton were compared based on ash-free dry mass and total chlorophyll. Macroinvertebrates between high and low-macrophytes sites were compared based on total and individual species standing biomass. Density, abundance, total length, and gut mass were compared between paired sites and diet preferences were also calculated. Data that represented percentages were arcsine transformed before paired t-tests were performed. Streams served as replicates (n=3) and results from individual sites were averaged to increase the accuracy of the replicates.

Food Web Construction

Stable isotope analysis was conducted on periphyton, macrophyte, macroinvertebrate, slimy sculpin, and allochthanous detritus tissues from the low-macrophyte and high-macrophyte sites of Coon Creek. Delta values determined through IRMS were used to construct food webs based on the methods of Hershey *et al.* (2006). Bi-plots were used to represent the relationship between $\delta^{13}C$ and $\delta^{15}N$ values for each sample organism. When plotted, possible prey appeared to the left of and below the plotted point for each predator. Conversely, possible consumers of an organism appeared above and to the right of their respective prey. Peterson and Fry (1987) developed the standard trophic fraction assumption of between 3‰ and 4‰ for $\delta^{15}N$ and between 0‰ and 1‰ for $\delta^{13}C$. McCutchan *et al.* (2003) conducted a survey of literature values for trophic shift for stable isotopes of carbon and nitrogen. The average values from this survey were more specific estimations of 2.2 ± 0.18‰ for $\delta^{15}N$ and 0.5 ± 0.13‰ for $\delta^{13}C$. However, Post (2002) integrated multiple trophic pathways to his average fractionation estimation. In a food web setting, organisms likely feed on multiple prey items so incorporating multiple pathways into a fractionation estimate is important. Therefore, the values from Post (2002), 3.4 ± 1‰ for $\delta^{15}N$ and 0.4 ± 1.3‰ for $\delta^{13}C$ were used to create a liberal prediction region where organisms making up the majority of a sculpin's diet were expected to appear.

RESULTS

Physical Habitat

The low- and high-macrophyte sites did not differ significantly in thalweg velocity (t = -1.000, df = 2, p = 0.42), discharge (t = -1.853, df = 2, p = 0.21), wetted width (t = -0.599, df = 2, p = 0.61), depth (t = 0.414, df = 2, p = 0.72), or substrate size (t = 3.422, df = 2, p = 0.08). Water quality in the thalweg (i.e., temperature, dissolved oxygen, conductivity, and pH) were also not significantly different between low- and high macrophyte sites. The average riparian canopy cover at low-macrophyte sites was 57.7% ± 26.9, which was significantly different than the average canopy cover of 0.2% ± 0.0 at the high-macrophyte sites (t = 4.829, df = 2, p = 0.02, α = 0.05).

Macrophytes

When measured with 0.25 m^2 quadrats, average macrophyte cover was significantly greater in high-macrophyte sites than in low-macrophyte sites (t = -3.360, df = 2, p = 0.039, α = 0.05). The average standing biomass of submerged vegetation was greater in high-macrophyte sites than in low-macrophyte sites (t = -2.179, d = 2, p = 0.08, α = 0.10). Average biomass of submerged vegetation ranged from 232.5 to 6.8 g/m^2 between high- and low-macrophyte sites (Figure 2). One pair of sites had considerably more similar macrophyte biomass than the other two pairs. In general, high-macrophyte sites have greater macrophyte richness than low-macrophyte sites. Elodea (*Elodea canadensis*), water crowfoot (R*anunculus aquatilis*), and watercress (*Nasturtium officinale*) comprised most of the biomass in low-macrophyte sites and elodea, water crowfoot, watercress, horned pondweed (*Zannichellia palustris*), and an unidentified aquatic moss (Bryophyta) made up much of the biomass in the high-macrophyte sites.

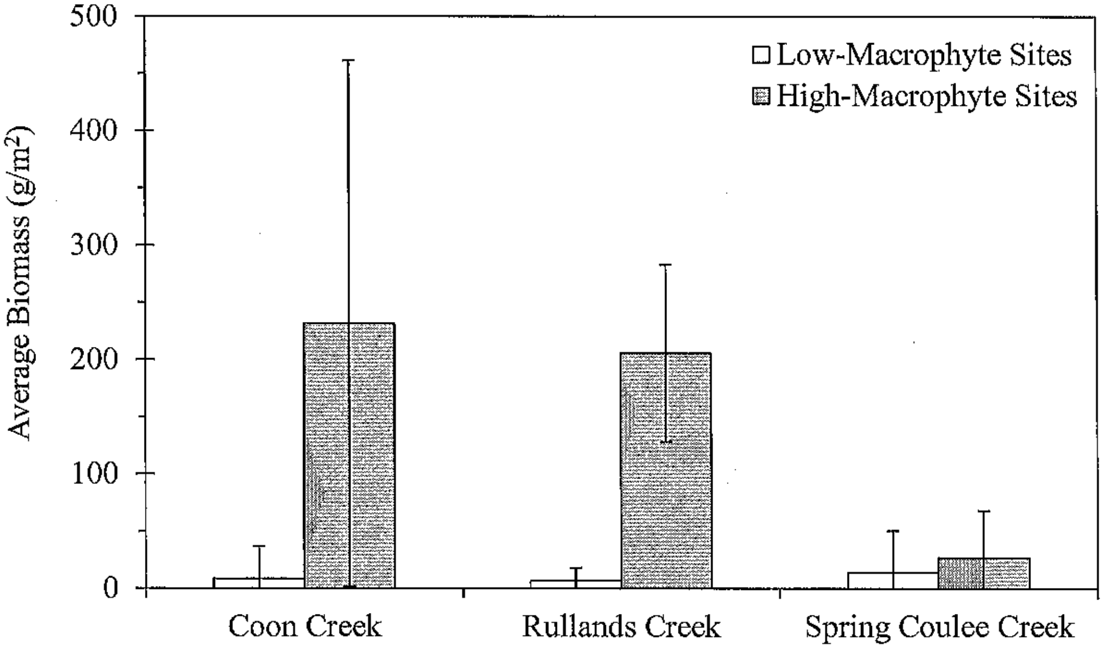

Figure 2. Average biomass (g/m^2 ± SD) of macrophytes in low- and high-macrophyte sites of three cold-water streams in western Wisconsin during the fall of 2012.

Periphyton

Ash-free dry mass and chlorophyll *a* biomass were not significantly higher in high-macrophyte sites than the low-macrophyte sites (afdm: $t = -0.211$, $df = 2$, $p = 0.43$, chl *a*: $t = 0.46$, $df = 2$, $p = 0.35$). Average ash-free dry mass ranged from 1.6 to 10 mg/cm^2 in low- and high-macrophyte sites in the three study streams. Average chlorophyll *a* biomass was around 0.09 to 0.11 g/m^2.

Macroinvertebrates

Of ten macroinvertebrate taxa examined, standing biomass and density were not significantly different between low- and high-macrophyte sites. Brachycentridae represented the family with the greatest average standing biomass in low- and high-macrophyte sites, 2.51 g/m^2 and 0.83 g/m^2, respectively. Brachycentridae, Gammaridae, Elmidae larvae, and Hydropsychidae represented the groups with the largest standing biomass in high-macrophyte sites, while Brachycentridae, Hydropsychidae and Gammaridae were greatest in low-macrophyte sites (Figure 3). Baetidae, Hydropsychidae, and Chironomidae had the highest densities at low-macrophyte sites and Brachycentridae, Elmidae (larvae), and Gammaridae were the densest taxa at high-macrophyte sites (Figure 4).

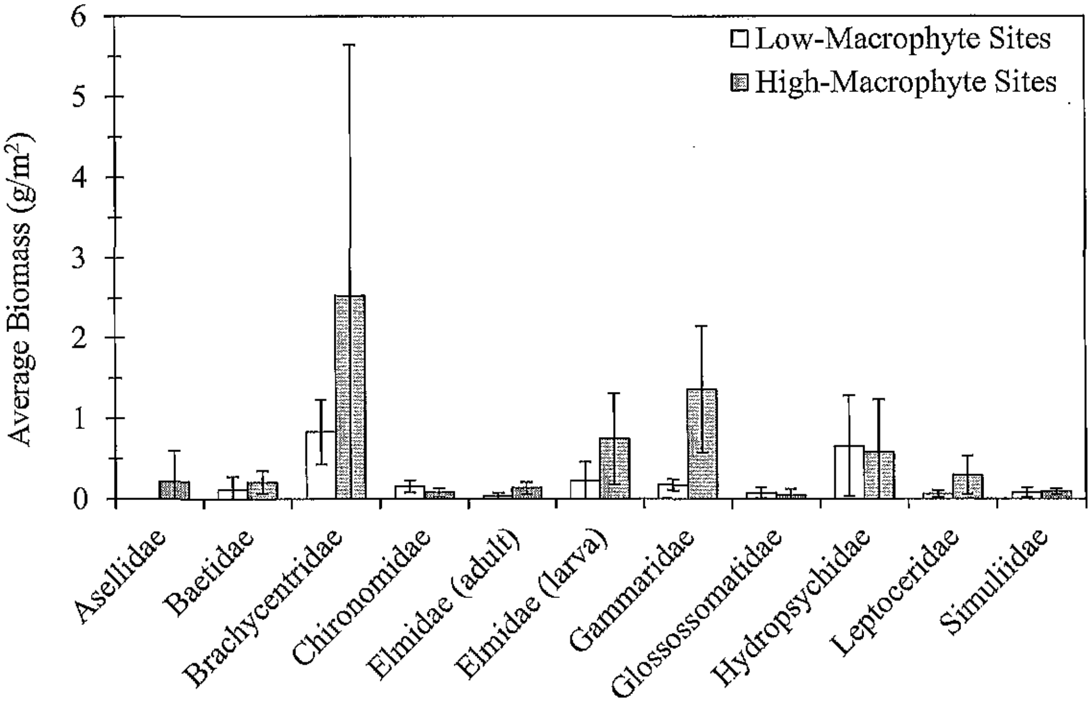

Figure 3. Average biomass (g/m^2 ± SD) of macroinvertebrate families in low- and high-macrophyte sites of three cold-water streams in western Wisconsin during the fall of 2012.

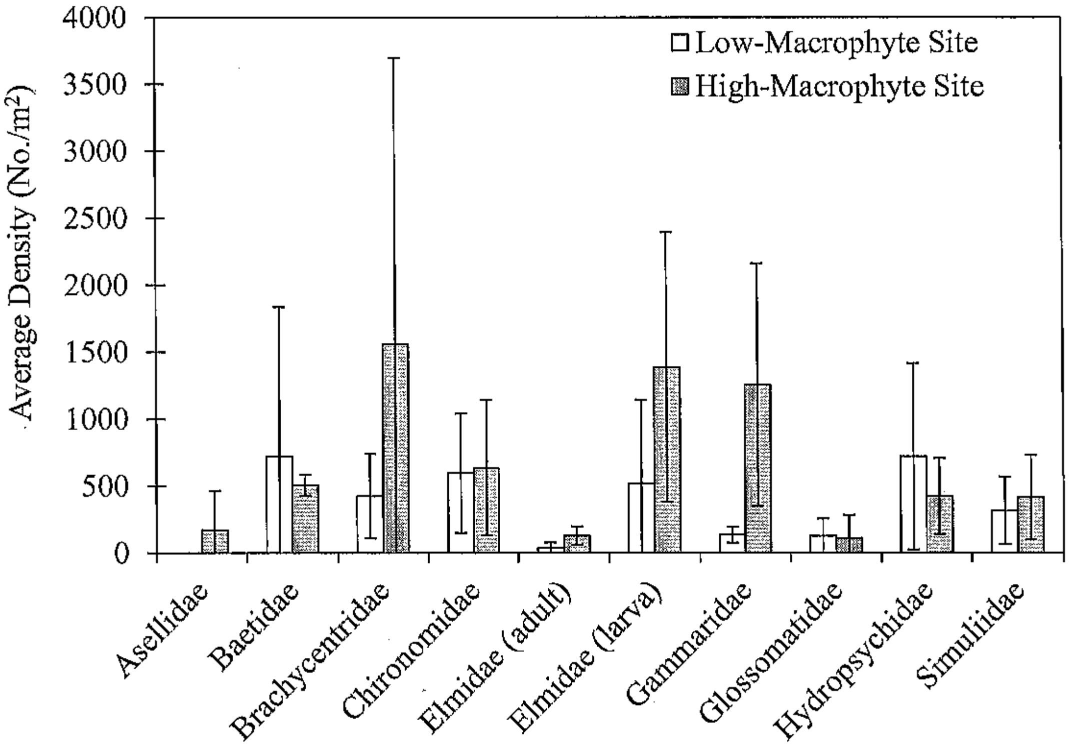

Figure 4. Average density (No./m^2 ± SD) of macroinvertebrate families in low- and high-macrophyte sites of three cold-water streams in western Wisconsin during the fall of 2012.

Slimy Sculpin

Analysis of the average length of slimy sculpin captured in low- and high-macrophyte sites revealed that the mean length of sculpin at low-macrophyte sites was not significantly different than those at high-macrophyte sites ($t = -1.516$, $df = 2$, $p = 0.27$). Conversely, the average total density at high-macrophyte sites (1.2 ± 0.1 fish/m^2) was significantly higher than sculpin density at low-macrophyte sites (0.7 ± 0.1 fish/m^2; $t = -5.000$, $df = 2$, $p = 0.02$). Despite this, the density of small-bodied sculpin (<5 cm) was not significantly different between site types, nor was the percentage of the captured population that was made up of small-bodied sculpin (Figure 5).

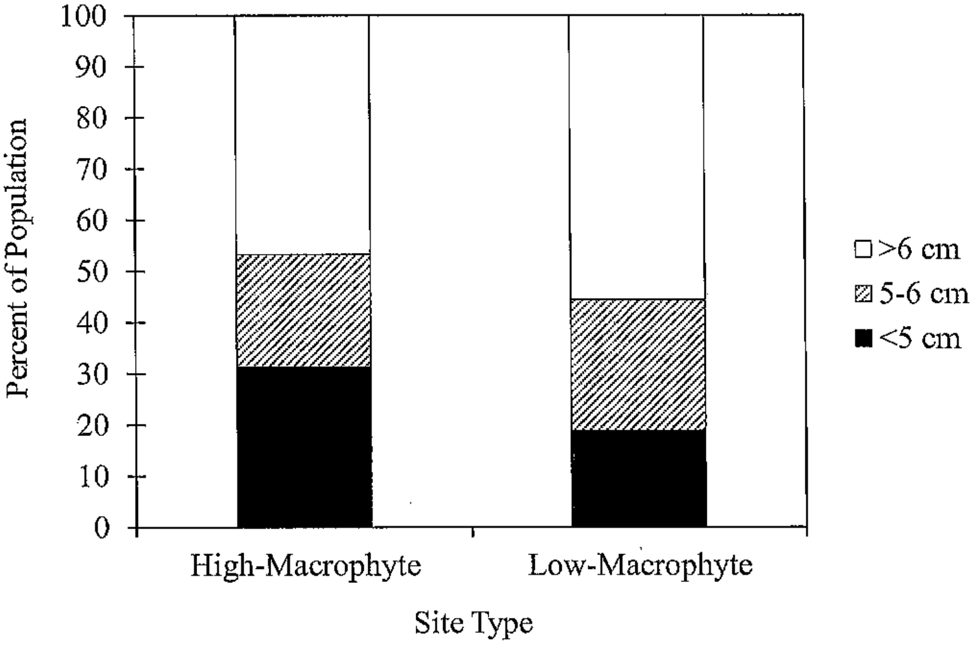

Figure 5. Average percent of slimy sculpin population represented by three size groups, >6 cm, 5-6 cm, and <5 cm in high- and low-macrophyte sites in cold-water streams in western Wisconsin.

When the food masses contained in sculpin guts were corrected for the length of the individual, the sculpin collected from high-macrophyte sites contained significantly more food in their guts than sculpin from low-macrophyte sites ($t = -5.100$, $df = 2$, $p = 0.02$). The percentage of sculpin containing the larvae in the family Baetidae in their guts was not significantly different between site types (Figure 6). However, the percentage of sculpin with Gammaridae in their guts was significantly different between high- and low-macrophyte sites ($t = -6.613$, $df = 2$, $p = 0.02$). Also, the percentage of captured sculpin with empty stomachs was significantly less in high-macrophyte sites than in low-macrophyte sites ($t = 8.503$, $df = 2$, $p = 0.014$).

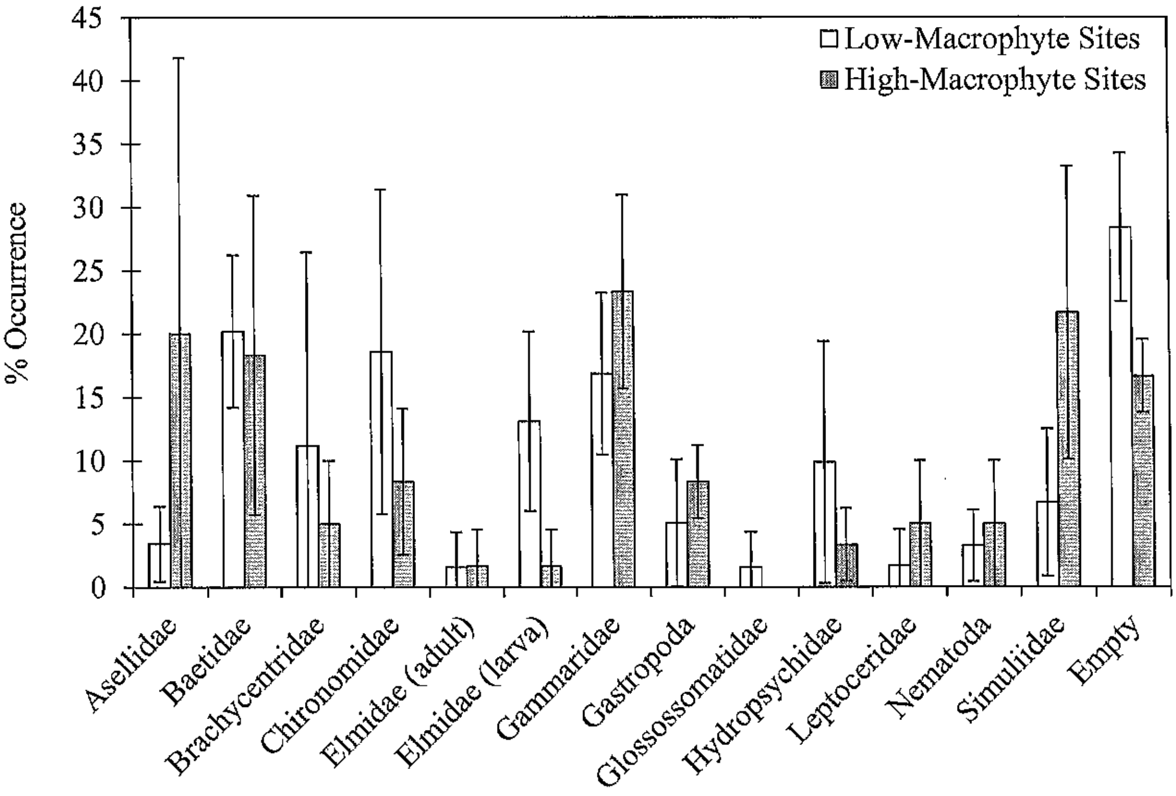

Figure 6. Average percentage (± SD) of slimy sculpin, from low- and high-macrophyte sites, containing various macroinvertebrate food items in their gut. Sixty sculpin gut samples were examined from each site type.

In the high-macrophyte sites, Asellidae was the only taxon which sculpin showed high selective preference (Table 1). In low-macrophyte sites, sculpin showed active selection for Baetidae, Asellidae, and Gammaridae, although only moderately. Sculpin showed complete avoidance of Leptoceridae in low-macrophyte sites and nearly complete avoidance of Elmidae larvae in high-macrophyte sites. Ivlev values near 0 indicate that the prey item was being consumed in a proportion similar to what is available in the environment. Chironomidae, Elmidae larvae and Simuliidae were consumed this way in low-macrophyte sites, while Gammaridae and Chironomidae had values near zero in high-macrophyte sites.

Table 1. Ivlev's Electivity Index (E_i) as calculated for ten macroinvertebrate taxa at low- and high-macrophyte sites in three cold-water, western Wisconsin streams during the fall of 2012. Positive values indicate that selection is occurring and negative values indicate avoidance is occurring. A value of 1 or -1 indicates complete preference or avoidance, respectively, whereas 0 means no selection is occurring and that the number consumed is proportional to the number available.

	E_i	
	Low	High
Baetidae	0.39	0.20
Asellidae	0.33	0.93
Gammaridae	0.32	0.09
Chironomidae	0.15	-0.02
Elmidae (larvae)	0.01	-0.91
Simuliidae	-0.04	0.53
Glossossomatidae	-0.24	-0.67
Elmidae (adult)	-0.63	-0.76
Brachycentridae	-0.74	-0.74
Hydropsychidae	-0.74	-0.71
Leptoceridae	-1.00	-0.46

Food Web

Due to low biomass upon collection of several taxa, not all desired macroinvertebrate groups were able to be analyzed for stable isotopes of carbon and nitrogen. Of the ten targeted taxa, seven were analyzed from the high-macrophyte site in Coon Creek and six were analyzed from the low-macrophyte site (Table 2).

Table 2. Macroinvertebrate taxa that were present in (Y) or absent from (N) carbon and nitrogen stable isotope analysis. Organisms were collected from low- and high-macrophyte sites in Coon Creek of western Wisconsin.

Taxon	Low	High
Brachycentridae	Y	Y
Elmidae (larvae)	Y	Y
Gammaridae	Y	Y
Simuliidae	Y	Y
Baetidae	Y	N
Chironomidae	Y	N
Aesellidae	N	Y
Glossossomatidae	N	Y
Hydropsychidae	N	Y

In addition, allochthonous detrital matter was not encountered in the high-macrophyte site and therefore was not analyzed for stable isotopes. With the exception of Brachycentridae, the macroinvertebrates at the high-macrophyte site were more enriched in ^{13}C and were fairly equal in ^{15}N, than organisms at the low-macrophyte site (Table 3; Figure 7).

Periphyton signatures were similar in that they were more enriched in ^{13}C than any of the other organisms analyzed (Figures 7). However, the periphyton at the high-macrophyte site was more enriched in ^{13}C than the low-macrophyte site. The level of ^{15}N enrichment was similar for periphyton between sites. In the low-macrophyte sites allochthonous detritus represented the group that was the most depleted in ^{15}N. There were only two macrophyte types encountered at this site, Elodea and curly-leaf

Table 3. Results of stable isotope analysis for carbon (δ13C) and nitrogen (δ15N) of aquatic organisms in low-and high-macrophyte sites of Coon Creek in western Wisconsin during the fall of 2012. Values represent averages in parts per thousand (‰) ± standard deviation.

	δ^{15}N (‰)		δ^{13}C (‰)	
Category of matter	Low	High	Low	High
DETRITUS	1.37±0.14	-	-28.82±0.12	-
PERIPHYTON	3.88±0.54	2.88±0.29	-22.07±1.17	-18.6±1.62
MACROPHYTE				
Elodea	6.9±0.12	5.4±0.07	-34.95±0.17	-31.59±0.07
Water Crowfoot	-	3.58±0.13	-	-27.25±0.08
Watercress	-	5.35±0.03	-	-29.72±0.11
Aquatic moss	-	5.21±0.25	-	-34.71±0.72
Horned pondweed	-	2.53±0.02	-	-26.22±0.47
Curley-leaf pondweed	4.99±0.07	5.51±0.03	-34.97±0.32	-29.82±0.05
MACROINVERTEBRATE				
Baetidae	5.42±0	-	-32.59±0	-
Brachycentridae	6.1±0.01	8.29±0.19	-33.59±0.03	-30.69±0.09
Chironomidae	6.05±0.05	-	-29.47±0.03	-
Elmidae (larvae)	3.88±0	5.06±1.66	-36.33±0	-25.75±14.97
Glossossomatidae	-	5.34±0.01	-	-31.34±0.01
Hydropsychidae	-	3.52±0.02	-	-36.35±0.12
Asellidae	-	4.92±0.07	-	-28.91±0.14
Gammaridae	5.85±0.1	4.46±0.08	-28.65±0.02	-27.96±0.03
Simuliidae	5.51±0	5±0	-28.62±0	-29.41±0
SLIMY SCULPIN				
<5 cm total length	10.04±0.47	9.79±0.65	-30.36±0.5	-30.29±0.78
>6 cm total length	9.36±0.41	8.57±0.13	-28.83±0.78	-29.77±1.16

pondweed. Compared to these same vegetation type in the high-macrophyte sites, Elodea at the low-macrophyte site was more enriched in ^{15}N, but more depleted in ^{13}C and curly-leaf pondweed was more depleted for both isotope than those at the high-macrophyte site. The high-macrophyte site had a greater richness of macrophytes. Horned pondweed and water crowfoot were the most depleted in ^{15}N, but the most enriched in ^{13}C, the aquatic moss was the most depleted in ^{13}C, and curly-leaf pondweed, Elodea, and watercress were the most enriched in ^{15}N.

For macroinvertebrates, there were no general patterns when similar taxa were compared between sites (Figures 7). The signatures of Brachycentridae were quite dissimilar between sites. At the low-macrophyte site Brachycentridae were enriched in ^{15}N by over 2‰ and enriched in ^{13}C by almost 2‰ compared to the high-macrophyte site. The ^{13}C signature of Elmidae larvae was more enriched in the low-macrophyte site, by about 1.5‰. Gammaridae and Simuliidae were the only other comparable taxa because they were sampled at both site types. These families showed fairly similar isotopic signatures between low- and high-macrophyte sites. Hydropsychidae had isotopic signatures similar to Elmidae larvae, Asellidae were similar to Simuliidae, and Glossossomatidae were similar to Elodea. At low-macrophyte sites baetidae had isotopic signatures between Brachycentridae and Elmidae larvae, while chironomidae were more similar to Simuliidae and Gammaridae.

Slimy sculpin had very similar isotopic signatures between sites (Figures 7). At both sites on average, small sculpin (<5 cm) were more enriched in ^{13}C and more depleted in ^{15}N than large sculpin (>6 cm). Sculpin at the low-macrophyte site were slightly more enriched in ^{15}N than those from the high-macrophyte site.

When calculations were made to predict the areas of the plot where the sculpins' food source should appear, there was more overlap in the small sculpin and large sculpin diet predictions at the low-macrophyte site than at the high-macrophyte site (Figures 7). In the high-macrophyte sites, large sculpin were predicted to prey upon Simuliidae, Asellidae, and Glossossomatidae, while at low-macrophyte sites, Chironomidae and

Baetidae were predicted prey. Prey items of small sculpin were predicted to be the same as large sculpin in high-macrophyte sites, with the addition of Gammaridae. Gamarridae, Simuliidae, and Chironomidae were predicted prey items for small sculpin in the high-macrophyte sites.

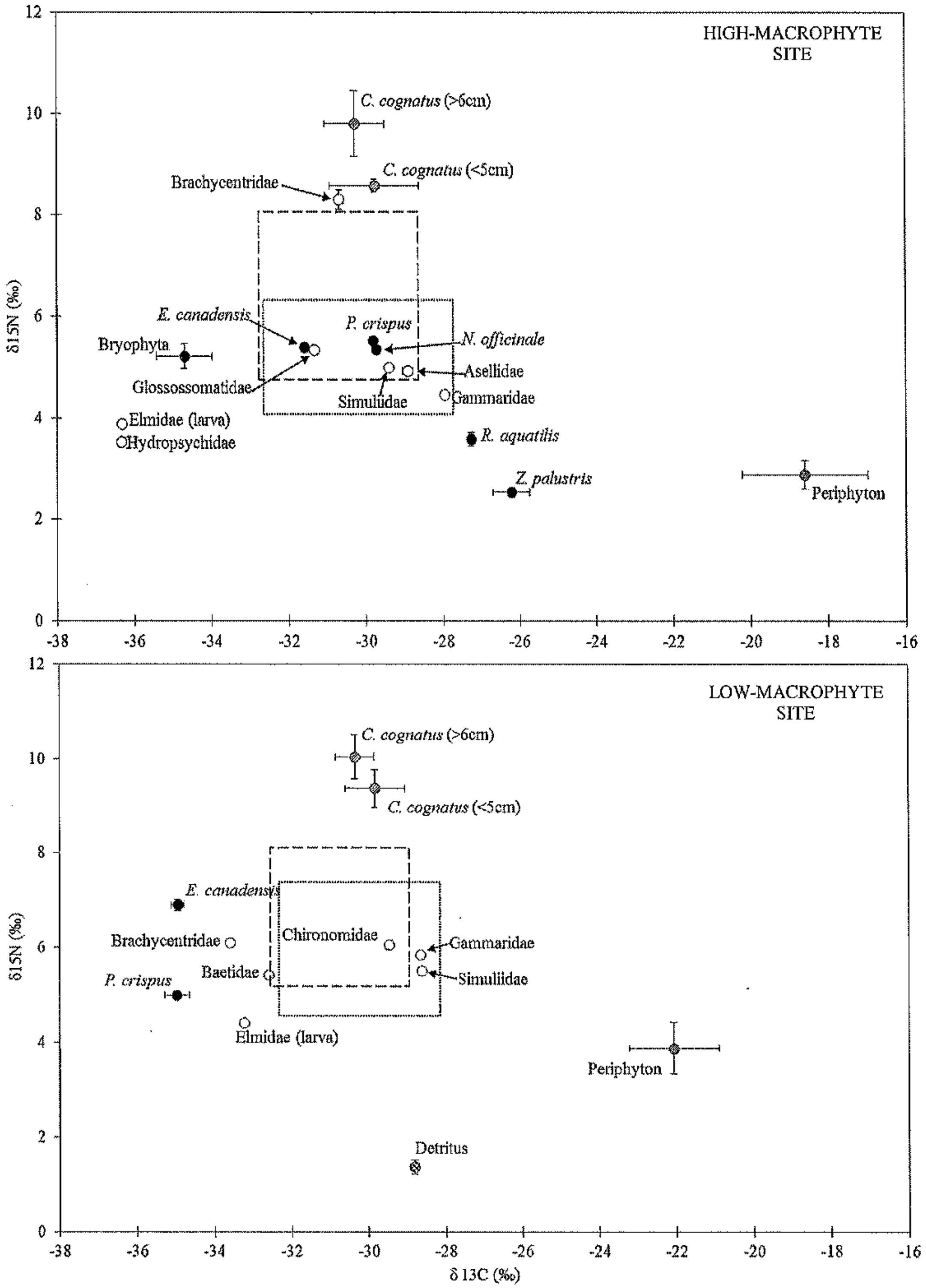

Figure 7. Results of carbon and nitrogen stable isotope analysis of stream organisms from high- and low-macrophyte sites of Coon Creek during the fall of 2012. Isotopic signatures were measured as $\delta^{15}N$ and $\delta^{13}C$ (‰) values (± SD). Dashed boxes represent the predicted regions for isotopic signatures of large sculpin (>6cm) prey. Dotted boxes represent the predicted regions for isotope signatures of small sculpin (<5cm) prey. Prediction regions were calculated using values from Post (2002).

DISCUSSION

Macrophyte cover was significantly greater in areas with minimal canopy cover (high-macrophyte sites) versus sites with denser canopy cover (low-macrophyte sites). The lack of riparian tree cover allows more light for aquatic plants and in high-macrophyte sites, this resulted in more vegetation coverage of the stream bed. The biomass of macrophytes was also higher in open-canopy sites when compared to closed-canopy sites. Again, the increased availability of light for photosynthesis at high-macrophyte sites allows a longer daily growth period for submerged plants and also potentially longer growing season as sunlight may warm waters during the day longer into the fall and earlier in the spring at open canopy sites. More solar energy into the system drives more primary production, allowing macrophytes to grow more abundantly (Cummins 1974). Open canopy sites also hosted a macrophyte community with greater species richness, possibly due to the less light-limited environment. Also, all high-macrophyte, open-canopy locations occurred in areas that were highly grazed by cattle and were likely subject to much greater nitrogen loading than low-macrophyte sites. This may have contributed to greater macrophyte cover, biomass and species richness observed at these sites.

Assuming that light availability promotes primary production, epilithic periphyton biomass was expected to be greater at high-macrophytes sites. Therefore, it was surprising that no significant difference was observed between site types. Although periphyton, which is composed in part of microalgae, has been shown to have increased growth in response to greater light availability (Davis 2002; Hill and Fanta 2008; Rowell and Sobczak 2008; Sanches *et al.* 2011), it is in direct competition with other primary producers, like macrophytes, where light is abundant. The shading effects of macrophytes may have decreased the biomass of periphyton in the high-macrophyte sites to the extent that riparian vegetation shades stream substrate in low-macrophyte sites. The lack of differences in periphyton biomasss was also found in previous studies in the same study basin (Laukkanen 2012) and a study by Inoue and Nunokawa (2005) in Japan to which the later suggested that there are numerous factors contributing to primary production in streams that are site-specific and cannot be based on just one factor (e.g. light availability). Also, only epilithic periphyton was considered in this study; epiphytic periphyton may be much more abundant than epilithic in high-macrophyte areas because the surface of the macrophytes could be the dominant growing surface.

Not only was epilithic periphyton growth similar with and without macrophyte growth, the densities and standing biomass of common macroinvertebrate taxa were not different between site types either, which contradicted my original hypothesis. While these results are consistent with an unpublished study that was also conducted within the Coon Creek watershed (Laukkanen 2012), they are inconsistent with other studies that find that both abundance and biomass of macroinvertebrates are higher in macrophyte beds (Collier *et al.* 1999; Hutchens *et al.* 2004; Shupryt and Stelzer 2009), however Shupryt and Stelzer (2009) found that higher macroinvertebrate abundance and biomass in macrophyte beds were influenced by time of year. In their study, invertebrate abundances decreased from the beginning of the year to the end in macrophyte beds and increased from the beginning of the year to the end in sites without macrophytes. Given that my study was conducted in September and October, it is probable that the site types exhibited similar abundances and biomass of invertebrate taxa due to the time of the year and likely display more pronounced differences during the spring and summer. Including seasonal changes into this study would have been beneficial in determining temporal changes in taxa abundances. It is also possible that there were simply not enough replicate paired sites to detect true invertebrate community differences between site types. Additionally, the lack of difference could have been due to the difficulty in separating epiphytic invertebrates from the macrophytes during sampling. Sculpin gut mass also contradicts the results of similarity of invertebrate abundance between site types. Individual sculpin sampled from sites with high-macrophyte growth (and higher sculpin density) had a more food in their guts than sculpin at the low-macrophyte (and lower sculpin density) sites. More food in the gut, combined with a larger number of sculpin feeding in the area does not seem feasible unless the high-macrophyte sites were hosting considerably more invertebrate prey than the site with low macrophyte cover.

The number of taxa observed between site types was also very similar, which is consistent with the findings of other researchers that macrophyte beds do not seem to impact the diversity of the invertebrate community as much as they support increased biomass and abundance (Hutchens *et al.* 2004; Shupryt and Stelzer 2009). However, several studies have found greater species richness in riverine systems where macrophytes dominate versus where they are scarce (Wright 1992; Gregg and Rose 1985).

Sculpin were not segregated by size between sites as hypothesized. I expected that small-bodied sculpin (<5cm) would make up a larger proportion of the population in areas with high macrophyte cover, but instead it appears that total density of slimy sculpin was affected by macrophyte abundance. It has been shown that sculpin density and habitat choice can be influence by a number of factors including: invertebrate prey abundance (Petty and Grossman 2010), intra-specific competition (Davey *et al.* 2005), predation (Chivers *et al.* 2001), as well as physical stream parameters like temperature (Scott and Crossman 1979; Lyons 1990). General stream parameters were similar between site types, as were macroinvertebrate (i.e., prey) abundances, suggesting food availability and stream parameters were not influencing habitat choice at the scale of the study sites. Also, large and small sculpin were not segregated (i.e., there was no difference in the average size (total length) of sculpin between site types), which indicates that at the time of sampling, intra-specific competition was likely not driving habitat choice. Predation was the most likely driver of the higher abundance of sculpin that was observed in high-macrophyte sites. Even though it has been shown that sculpin prefer rocky substrates that are more abundantly characteristic in the low-macrophyte sites, there is little cover from predators in these areas. Meredith *et al.* (2015) found that sculpin densities were strongly correlated with brown trout (*Salmo trutta*) and cutthroat trout (*Oncorhynchus clarkii*) abundances in a lotic system in Utah. All streams examined in this study are thriving trout streams and host healthy, reproducing brown trout and brook trout (*Salvelinus fontinalis*) populations. Macrophyte abundance played a role in the distribution of slimy sculping by providing areas of shelter and refuge from large, piscivorous predators.

Sculpin prey selection also indicates that sculpin are feeding in macrophyte beds more often than on cobbled substrate. Even though abundance of each taxa was not different between the site types, Ivlev's Electivity Index values show that sculpin in high-macrophyte sites show a strong preference for Asellidae, which is commonly found in vegetation patches and root mats (Bouchard 2004). Asellidae, Baetidae, and Gammaridae were moderately selected for in low-macrophyte sites. While these taxa can be associated with macrophytes beds, this study took place in the early fall, so the input of allochthonous detritus to forested stream reaches allows for an increase in these shredder, collector, and gatherer taxa even though there was minimal autochthanous vegetation available.

While the results of the Ivlev's Electivity Index calculations should be accepted with some caution due to the lower than recommended sample size of sculpin stomachs examined, Mundahl *et al.* (2012a) found that sculpin from cold-water streams in southeastern Minnesota selected for Asellidae, Gammaridae, and Baetidae, and avoided Brachycentridae and Gastropoda. These findings are very consistent with the selectivity found in my study and characteristics of sculpin feeding behavior further support why sculpin may feed in macrophyte beds. First, sculpin have been shown to use macroinvertebrate abundance as a factor in choosing sites to occupy (Petty and Grossman, 1996) and sculpin are also able to shift their diet to accommodate seasonal changes in the invertebrate community (Owens and Dittman 2003; Hondorp *et al.* 2005). As fall approaches, macrophyte beds begin to senesce, which may stimulate an increase in Gammaridae and Asellidae abundance. Sculpin prey selection may occur in response to this increased abundance for these taxa. Second, sculpin often feed in areas where they must use their lateral line to detect prey items rather than sight (Kanter and Coombs 2003). Prey that move more frequently or exercise larger movements are more likely to be detected by sculpin (Kratz and Vinyard 1981). So, while Brachycentridae and Hydropsychidae may be abundant compared to other taxa in both stream types, their location on rocky substrate in open flow areas is coupled with a stationary life-style and appearance which might make them undetectable to sculpin and unattainable in fast-flow stream sections, resulting in avoidance. Asellidae and Gammaridae are much more mobile and often larger bodied so they are more likely to be detected by sculpin. Macrophytes tend to slow water velocity due to increased frictional forces, so not only can mobile prey items accumulate in macrophyte beds, but sculpin can easily feed in these slow-velocity oases. Additionally, Gammaridae have large bodies, high mobility, abundance, and residence in the shelter of macrophytes, which combine to make them an easy prey item. Similarly, in low-macrophyte sites their size and mobility allows them to be preferentially detected and selected by sculpin more than a less mobile prey item even though they are not as abundant. Last, the feeding behavior most relevant to the findings of this study may be that sculpin have been shown to choose taxa based on accessibility and the balance between the benefits of larger prey items and the risk of predation (Kratz and Vinyard 1981). Sculpin show positive selection towards invertebrates associated with macrophyte beds and there are more sculpin per area in high-macrophyte sites, so it is likely that sculpin choose to feed in vegetation because of the relative ease of prey capture and low risk of predation.

The apparent effects of macrophyte abundance on the density of slimy sculpin seem to stem from predator-prey interactions and prey accessibility due to seasonal changes in abundant taxa rather than overt differences in food web structure. This was further supported by the isotope data from Coon Creek, which showed similar food web structure between site types. Food webs at both high- and low-macrophyte sites clearly did not depend on the primary production of periphyton as a carbon source to the system and instead depended on the decay of vegetative matter. Detritus at high-macrophytes sites likely had both terrestrial and aquatic origins, while detritus at low-macrophytes was terrestrial based. Neither detritus of terrestrial nor aquatic origin were analyzed for stable isotopes in the high-macrophyte locations, however terrestrial detritus is likely similar in the high-macrophyte locations as in the low-macrophyte locations, albeit less abundant. Detritus from senescing macrophytes would be more abundant in the high macrophyte locations, especially as the fall months progress. It has been demonstrated that the stable isotope ratios of aquatic vegetation change as a result of decomposition (Fellerhoff *et al.* 2003; Fourqurean and Schrlau 2003). Fellerhoff *et al.* (2003) found that δ^{15}N of macrophytes changed as much as 2-3‰ during the decomposition process and Fourqueam and Schrlau (2003) found a similar change as decomposition decreased the δ^{15}N of seagrass by 2‰. This was due to the colonization of and activity of microbes. If senescing and decompositing *Elodea canadensis*, which made up the majority of the macrophyte biomass in the high-macrophyte site of Coon Creek, was plotted with the decreased stable nitrogen isotope ratio, it would appear to be at the base of this high-macrophyte food web (Figure 8).

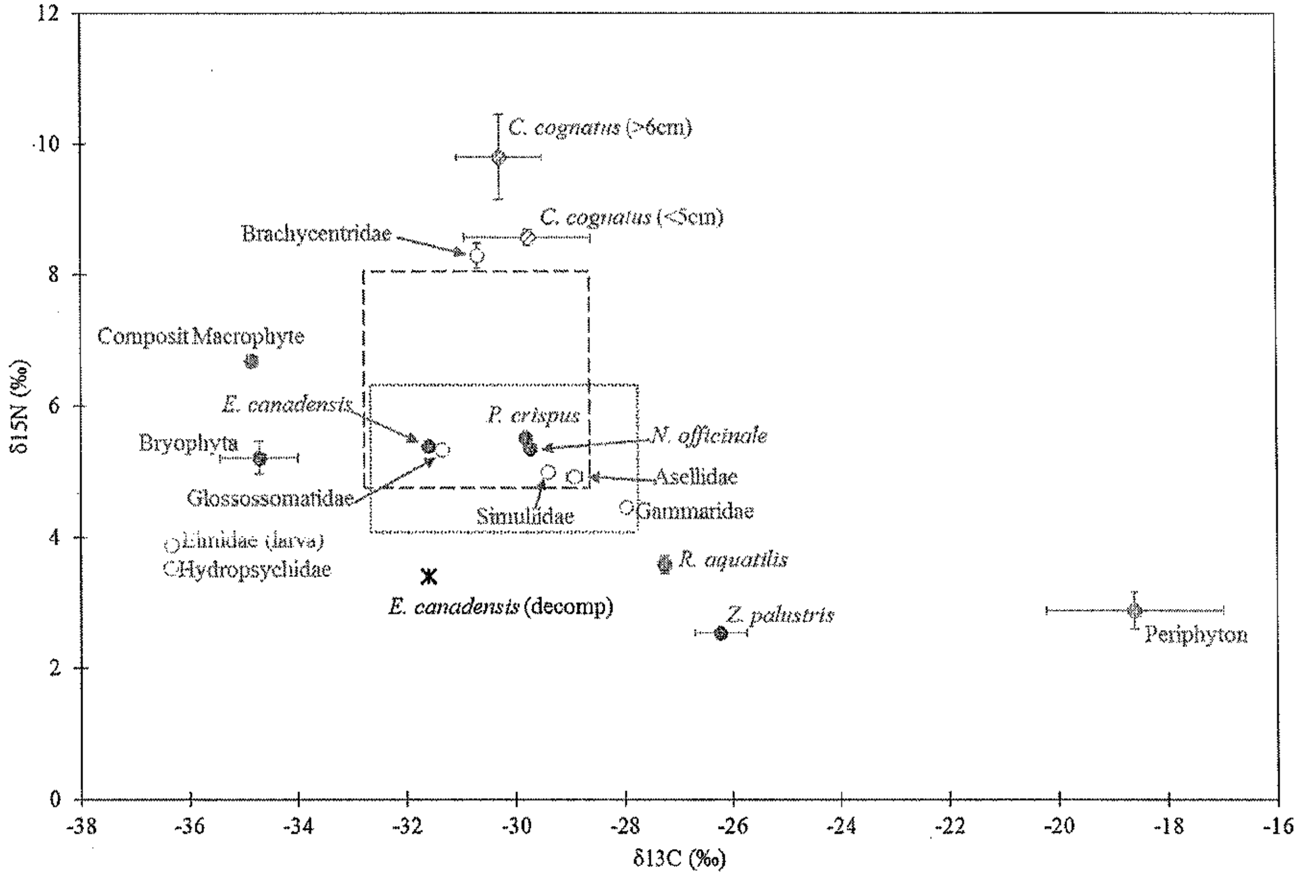

Figure 8. Estimated ratios of carbon and nitrogen stable isotopes for decomposing *E. canadensis* relative to analyzed ratios for other flora and fauna in a high-macrophyte site in Coon Creek during the fall of 2012. Ratio estimations were made using values from Fellerhoff *et al.* (2003) and Fourqurean and Schrlau (2003).

Sculpin feed predominantly on shredder and collector macroinvertebrate guilds in both sites and were predicted to feed on these taxa in the food web biplot. Due to the temporal influences on macroinvertebrate abundances and physical stream parameters these results are likely only reflective of the late summer or fall food-web dynamics in these cold-water streams.

This study highlights the importance of detritus, from both aquatic and terrestrial vegetation, as a carbon source in cold-water stream food webs, particularly in the fall and winter months when periphyton growth may decrease due to changes in irradiance

(Rosemond *et al.* 2000) and nutrient limitation (Francoeur *et al.* 1999). Changes in carbon source can have bottom-up effects on the food web by changing macroinvertebrate abundance and therefore prey choice for invertevores like slimy sculpin. Macrophyte abundance influences sculpin habitat choice by providing refuge from predators and macroinvertebrate prey during early fall in these cold-water stream habitats in western Wisconsin.

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