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thesis entitled

THE EFFECTS OF LAND USE ON LACUSTRINE WETLAND CHEMISTRY AND THE DIET OF BENTHIC CONSUMERS

presented by

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has been accepted towards fulfillment
of the requirements for the

M.S. degree in Zoology

Major Professor's Signature

August 8, 2007

Date

THE EFFECTS OF LAND USE ON LACUSTRINE WETLAND CHEMISTRY AND THE DIET OF BENTHIC CONSUMERS

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

2007

ABSTRACT

THE EFFECTS OF LAND USE ON LACUSTRINE WETLAND CHEMISTRY AND THE DIET OF BENTHIC CONSUMERS

By

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One of the most widespread effects of human activities on aquatic ecosystems is nutrient enrichment, which has been documented through traditional nutrient analyses and more recently, through the use of stable isotopes. However, little is known of nutrient effects on food webs in lacustrine wetlands. The objectives of this study were to (1) determine the effects of anthropogenic activities on nutrient concentrations in lacustrine wetlands, (2) assess how nitrogen stable isotopes vary with increasing exposure to human sources of nitrogen, (3) elucidate the relationships between food sources and invertebrate feeding groups among sites, (4) assess the importance of phytoplankton in consumer diets with increased nutrient enrichment, and (5) investigate the variability of stable isotopes at the site-specific level and the implications this has on food web analyses. My results indicated that urbanization affects wetland chemistry by significantly increasing total nitrogen and total phosphorus concentrations at impacted sites and increasing the $\delta^{15}N$ values of wetland biota. The diet of fingernail clams, snails, amphipods, and caenid mayflies could not be determined with stable isotopes. There were many complications in the identification of energy sources, include the variability of periphyton within sites, which I was able to identify in this study.

I would like to dedicate this thesis to my family for their endless encouraging words. I would especially like to dedicate this to my loving husband, Andrew, who has helped me throughout my master's project.

ACKNOWLEDGMENTS

I would like to thank the Michigan State University Department of Zoology for the opportunity to enhance my education. I would also like to acknowledge my committee members Dr. R. Jan Stevenson (Chairman), Dr. Stephen Hamilton, and Dr. Richard Merritt for their guidance throughout this research project. I would also like to thank Vanessa Lougheed for her field assistance and laboratory analysis of water samples and help with plant identification, Mollie MacIntosh for her help in the field and assistance in macroinvertebrate identification, and Christian Parker for his help in the field. Also, many thanks to Hasand Ghandi of the Stable Isotope Biogeochemistry Laboratory for analyzing my samples. This research was funded by The Great Lakes Fisheries Trust to R. Jan Stevenson et al. for "An Ecological Assessment of the Muskegon River Watershed to Solve and Prevent Environmental Problems."

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INTRODUCTION

Anthropogenic influences have altered the global nitrogen (N) and phosphorus (P) cycles. Some common disturbances to aquatic systems include the addition of wastewater effluent, increased sedimentation resulting from agricultural practices or urbanization, and the application of fertilizers that enrich runoff and groundwater (Bennett *et al.* 2001). Each of these common practices results in increased nutrient loads to aquatic ecosystems. As available nutrients increase, there is an increase in primary production - a process known as eutrophication. In lentic ecosystems, phytoplankton biomass can increase to a point where light attenuation inhibits the growth of benthic aquatic macrophytes (Wetzel 2001). This shift in primary production and biomass can accordingly impact the diet of primary consumers. In this study, I sought to determine the impacts of land use on wetland nutrient chemistry and, in turn, on trophic interactions.

According to Owen *et al.* (1998), wetland functions fall into three main categories: wildlife habitat, hydrologic processes, and water quality improvement. Many wildlife species require wetlands for at least a part of their life cycles. They also provide a variety of flora, fauna, and feeding niches for numerous organisms. Hydrologically, wetlands are important for flood mitigation and aquifer recharge (Mitsch and Gosselink 2000, Owen 1998). The land-water interface links the hydrologic processes with chemical processes. Where groundwater and surface water runoff travel through fringing wetlands before reaching a lake, the wetlands may remove nutrients and contaminants (Mitsch

and Gosselink 2000). This results in wetlands being more susceptible to anthropogenic contamination than the lake itself. Mitsch (1992) described wetlands as the "buffer between uplands and lakes." The impacts of human-derived nutrients on wetland nutrient chemistry have been widely studied using traditional nutrient analysis and stable isotopes (Carpenter *et al.* 1998; McClelland and Valiela 1998), but less is known of the human impacts on food webs in wetlands.

Stable isotope chemistry has become a widely used tool in recent years for ecological studies, including determining food web structure, because it takes into account what is actually assimilated into the tissues of the consumer. This is unlike traditional gut content analyses that are indicative of everything that is ingested, not just what is nutritionally available for the organism. Stable isotopes are interpreted by comparing the ratio of the amount of a heavy isotope to its corresponding lighter isotope in tissues of consumers relative to potential food sources after incorporating isotopic fractionation that occurs between trophic steps.

Food web studies often incorporate stable isotope analysis of carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N). Carbon isotopic ratios of animals typically reflect that of their diet, increasing less than 1‰ per trophic level (Michener and Schell 1994; DeNiro and Epstein 1978). The nitrogen isotopic ratios of animals are typically enriched by an average of 3 to 5‰ (Peterson and Fry 1987). Thus, the combined use of carbon and nitrogen stable isotopes can be a powerful tool

in assessing food sources and food web structure. Therefore, I chose this method for analyzing the diets of specific primary consumers in this study.

Consumers can be categorized by their functional feeding group. For aquatic macroinvertebrates this is generally dependent on animal morphology because this controls how and what an organism can consume (Merritt and Cummins 1996). Bivalves are filter feeders and their isotopic signatures should reflect that of a diet of phytoplankton and other seston found in the water column (Vaughn and Hakenkamp 2001). Due to their abundance, I studied the diet of fingernail clams (family Sphaeriidae). Gastropods are scrapers, which are adapted for removing attached algae from substrates (Cummins 1974), so I expected to see their diet consistent with periphyton consumption. The snails studied included Lymnaeidae, Physidae, Planorbidae, and Viviparidae. The isotopic ratios of these clams and snails serve as a check of my methodology.

In many macroinvertebrates, there can be a shift in diet that is dependent on food source availability. Amphipods, from the class Crustacea, are more omnivorous in that they can utilize multiple food sources including detritus, filamentous algae, and animal material (Summers *et al.* 1997). Mayflies (Ephemeroptera) from the family Caenidae can be collector-filterers, collector-gatherers, or collector-gatherers/scrapers depending on genus. Therefore, they may feed on suspended or deposited fine particulate organic matter (FPOM) or attached material (Merritt and Cummins 1996). The study of these two organisms may provide insight into human-induced shifts in consumer diets.

Stable isotopes are also useful in determining sources of nutrient inputs. P has only one stable isotope and so I focused mainly on N as my tracer of anthropogenic influences. It has been shown that anthropogenic N, either from human or animal waste is isotopically heavier than N from natural sources (McClelland and Valiela 1997, Macko and Ostrom 1994). Similar biota from two separate systems, where one is more urbanized and receiving wastewater inputs and the other is considered "pristine," often will have different $\delta^{15}N$ signatures, with higher $\delta^{15}N$ values in the biota from the system receiving wastewater inputs. Knowing this, I can compare the biota between sites to determine which sites are most affected by anthropogenic nutrient inputs.

In summary, primary production in wetlands is derived from plants and algae. Plants become more important for aquatic consumers as the decomposition process progresses and the plants are colonized by bacteria and fungi. Algae, on the other hand, are consumed directly by herbivores. I would hypothesize that algal production, specifically phytoplankton, would respond more than plant production in wetlands as nutrient enrichment increases. This should cause a shift in food webs that can be detected by stable isotope analysis.

The main objectives of this study were to:

(1) Determine the effects of anthropogenic activities on adjacent wetland nutrient concentrations.

(2) Assess how nitrogen stable isotopes vary with increasing exposure to human derived nitrogen sources.

(3) Elucidate the relationship between food sources and functional feeding groups, despite the variability in nitrogen stable isotope values among wetlands.

(4) Assess the importance of algae as the base of primary production for consumer diets with increased nutrient enrichment.

(5) Investigate the variability of stable isotopes at the site-specific level and assess the implications this has on food web analyses.

METHODS

Site Selection

In the summer of 2003, land use around lacustrine wetlands in Michigan was evaluated to determine which sites could be used as reference or degraded sites. Land use was used to distinguish reference and impacted sites based on the assumption that agricultural areas and highly developed areas increase the loading of nutrients to lacustrine wetlands. Sites were selected based on land use characterized by visual assessments of riparian land use and land use data from the National Land Cover Database 2001. Five sites were chosen to represent reference wetlands (Todd Lake, Otis Lake, Tubbs Lake, Ham Lake, and Leisure Lake) because they were located in primarily forested areas. Five impacted sites (Brooks Lake, Hillsview Lake, Mona Lake, Round Lake, and Wintergreen Lake) were chosen based on high levels of agricultural and urban land use. Brooks Lake had a high density of houses and summer cottages along its shoreline. Hillsview Lake and Round Lake were in areas with a combination of pasture land, row crops, and urban development. The Mona Lake watershed was highly urbanized. Wintergreen Lake was located within the Kellogg bird sanctuary, where it is known to be receiving high nutrient inputs from visiting waterfowl (Manny *et al.* 1994). All wetlands are located in the western to central portion of Michigan's Lower Peninsula (Figure 1).

To test the hypothesis that anthropogenic activities are affecting wetland nutrient chemistry, surface water was collected from the littoral zone for nutrient chemistry analysis in acid-washed bottles at each sample site. Total phosphorus

(TP) was determined using the ascorbic acid method following persulfate digestion (APHA 1998). Total nitrogen (TN) was analyzed by second-derivative UV spectroscopy analysis of nitrate (NO_3^-) following a persulfate digestion (Crumpton *et al.* 1992). These analyses were performed on a Skalar auto-analyzer.

Assessing links between land use and stable isotope signatures of producers and consumers

To determine if land use affected the isotopic signature of primary producers and primary consumers and to elucidate the relationship between sources and functional feeding groups, plants, epiphyton, suspended particulate organic matter (SPOM), and aquatic macroinvertebrates were collected.

Aquatic macroinvertebrates were collected using a standard D-net. They were then identified as far as possible in the field and sorted into separate glass jars with filtered wetland water. Each jar was placed in a cooler for 24 hours while the invertebrates cleared their gut contents, and then they were frozen. Gastropods and bivalves were pulled from their shells and identified based on their shell morphology.

The aquatic plants *Nuphar* spp. and *Nymphea* spp., which are dominant in the littoral zones of southern Michigan lakes, were collected from each site. Healthy petioles were collected with pruning shears and placed in plastic bags. To collect the epiphyton from these stems and leaves, deionized water was added to the bag and the plants rubbed vigorously until all epiphytes were

removed, and the resultant slurry was poured into 125 mL Nalgene bottles and frozen in the field.

Six 1-liter bottles of water were collected at random throughout the wetland for the analysis of suspended particulate organic matter (SPOM), which I am defining as the material found in the water column, which could include phytoplankton or seston. These were combined for one composite sample and water was filtered through two ashed 0.45µm glass-fiber filters. All of these filters were frozen immediately following filtration.

In preparation for carbon and nitrogen stable isotope analyses, all samples were placed in glass beakers, oven-dried at 60°C and treated with 10 % hydrochloric acid to avoid carbonate contamination. Lipids were removed from gastropods, bivalves, amphipods, and caenid mayflies using the Soxhlet extraction method with a chloroform/methanol solvent and dried again. The sample from each SPOM filter was scraped off using a razor blade and all samples were ground with a mortar and pestle for homogeneity. From each sample, a 0.5 to 1 milligram subsample was weighed into a tin capsule.

Stable isotope samples were analyzed at the Stable Isotope Biogeochemistry Laboratory in the Department of Zoology at Michigan State University. All samples were analyzed on either a VG Prism Series II Isotope Ratio Mass Spectrometer via dual inlet or a GV Instruments Isoprime Mass Spectrometer interfaced with a EuroVector Elemental Analyzer. The isotope ratios were expressed as $\delta^{13}C$ and $\delta^{15}N$ and referenced to a known standard, which is PeeDee Belemnite limestone for C and nitrogen gas in the atmosphere

for N. The values were expressed as $\delta^{13}C$ and $\delta^{15}N$ as per mil (‰). The δX values were calculated from the following equation where R is the ratio of the heavier isotope to the lighter isotope:

$$\delta X = [(R_{sample}/R_{standard})-1] \times 10^3$$ (Peterson and Fry 1987).

These data were used to test the following three hypotheses: isotopic ratios of N will increase with increased anthropogenic activities in the watershed, there will be a clear producer-consumer relationship identifiable via stable isotope analysis, and phytoplankton will become a more important food web base as nutrient enrichment increases.

Assessing variability within sites

To investigate the hypothesis that variability of periphyton from different host species within one site is low relative to inter-lake variability and therefore not an important source for error, I chose one impacted site (Hess Lake) and one reference site (Todd Lake) in August 2004. From both of these sites I sampled the periphyton on five plant species and the fine particulate organic matter (FPOM) from the sediment surface. These samples were prepared for stable isotope analysis in the same way as the previous samples. All tests of statistical significance were performed using a two-sample *t* test with a 0.05 significance level.

RESULTS

In my assessment of the links between land use and lacustrine wetland chemistry, I found that wetland nutrient concentrations were affected by anthropogenic activities. The reference sites had significantly lower total nitrogen (TN) and lower total phosphorus (TP) than sites predicted to be impacted (Figure 2; P=0.0057 for TN; P=0.0331 for TP). For the reference sites, TN ranged from 434.8 to 1046.8 µg/L with a mean=723.5 µg/L and TP ranged from 9.3 to 23.3 µg/L with a mean=17.7 µg/L. For the impacted sites, TN ranged from 1018.6 to 1441.4 µg/L with a mean of 1195.0 µg/L and TP ranged from 34.3 to 119.2 µg/L with a mean of 58.5 µg/L. This is consistent with other lacustrine wetland nutrient data from the Muskegon River Watershed Ecological Assessment Project (2004) which found TN ranging from 420 to 1620 µg/L and TP ranging from 4.7 to 35.1 µg/L.

To assess the links between land use and the stable isotope signatures of producers and consumers, I averaged similar biota for reference sites and impacted sites. Land use did affect the $\delta^{15}N$ value of primary producers and consumers (Figure 3). For the reference sites, mean $\delta^{15}N$ ranged from 0.54 to 3.50‰ versus 3.17 to 8.69‰ for the impacted sites. I concluded that there was a statistically significant increase in $\delta^{15}N$ in impacted sites compared to reference sites for epiphyton-*Nuphar* spp. (P=0.0027), amphipods (P=0.0016), caenids (P=0.0156), gastropods (P=0.0039), and SPOM, which was presumably manly phytoplankton (P=0.0480). Although the impacted sites have higher $\delta^{15}N$ values

for epiphyton-*Nymphea* spp. (P=0.0904) and bivalves (P=0.2456), the differences were not statistically significant.

Using stable isotopes, I was unable to determine the relationships between the producers and consumers chosen for this study or determine the importance of algae as nutrient enrichment increases. Bivalves and gastropods have very specific feeding habitats, so I expected to see clear relationships between these organisms and their expected diet. For all sites where bivalves were present, there appeared to be no relationship between the $\delta^{15}N$ and $\delta^{13}C$ values of bivalves and SPOM (Figures 4 and 5). At nine sites, the $\delta^{15}N$ and $\delta^{13}C$ values for gastropods did not reflect that of their predicted diet of periphyton (Figures 6 and 7). In Wintergreen Lake, however, epiphyton was a possible primary food source for gastropods based on predicted trophic fractionation (+1‰ for $\delta^{13}C$, +3-5‰ for $\delta^{15}N$).

Mayflies and amphipods span a range of functional feeding groups and therefore were used to assess the importance of algae in the food web. There appeared to be no significant relationships between amphipods, caenids, and the sampled epiphyton or SPOM for any site (Figures 8 and 9). These results indicate that there are other variables to consider when performing diet analyses using stable isotopes. This is explored further in the discussion section.

All consumers were analyzed against their predicted diet to determine whether their $\delta^{15}N$ and $\delta^{13}C$ values were greater than that of the food sources. Each relationship was analyzed by plotting the mean shift between each consumer and its expected food sources for reference and impacted sites

(Figures 10, 11, 12, and 13). T-tests were performed to determine whether any of these difference were significantly greater than 0, where I looked for $P<0.05$ and $t>t_{critical}$. The mean difference between each consumer and potential food sources previously discussed was not significantly greater than 0, except for the mean difference in $\delta^{15}N$ between amphipods and SPOM at the impacted sites ($P=0.016$, $t=3.80$, $t_{critical}=2.35$). I also assessed the relationship between epiphyton and SPOM (Figure 14) for all sites together. The mean $\delta^{15}N$ signature for epiphyton (*Nuphar spp.* and *Nymphea spp.* averaged together) (4.37) was significantly greater than the mean $\delta^{15}N$ signature for SPOM (2.63) ($P=0.017$, $t=2.48$, $t_{critical}=1.83$).

To assess the site level variability in stable isotopes analysis, I analyzed the periphyton from multiple substrata for one reference site (Todd Lake) and one impacted site (Brooks Lake) (Figure 15). For both sites, I collected fine particulate organic matter (FPOM) from the sediment surface and periphyton from five plants. The Todd Lake $\delta^{15}N$ values ranged from 1.3 to 6.4‰ and $\delta^{13}C$ values ranged from -11.3 to -28.8‰. For Brooks Lake the $\delta^{15}N$ values ranged from 1.6 to 4.7‰ and $\delta^{13}C$ values ranged from -24.5 to -26.7‰. This indicates a high level of variability within sites, although the source of variation was not determined.

DISCUSSION

Land use significantly affected wetland chemistry and allowed me to successfully identify reference and impacted wetlands. The anthropogenic contributions of nitrogen and phosphorus from urbanization and animal waste were reflected in the water chemistry at the impacted lacustrine wetland sites by significantly increasing TN and TP concentrations. These sources of nitrogen carry a greater $\delta^{15}N$ value that was incorporated into the tissues of the biota in the receiving waters, resulting in higher $\delta^{15}N$ values in the biota of the impacted sites compared to the reference sites. This pattern has been observed in many other systems, including Cape Cod estuaries (McClelland *et al.* 1997), streams (Northington and Hershey 2006), and lacustrine systems (Lake *et al.* 2001).

To determine whether land derived nutrients influenced the diets of primary consumers, I chose two organisms from very specific functional feeding groups, fingernail clams and snails. Fingernail clams are filter-feeders, so I expected their stable isotope data to reflect that of a diet consisting of SPOM. Since snails are scrapers, I hypothesized that they would be consuming mostly periphyton. My data did not support either of these hypotheses. There are numerous considerations for accurate data interpretation; I explore those further below.

Phytoplankton has been shown to be an important source of primary production in river (Peterson *et al.* 1993), as well as open water and coastal food webs (Keough *et al.* 1996). I collected phytoplankton from the water column and

concentrated the material onto filter paper. The downside of this method is that I was actually sampling everything in the water column and not just phytoplankton, hence referring to these samples as SPOM for this study. This could explain why the stable isotope data did not show that bivalves are consuming and assimilating SPOM. It is possible that bivalves are ingesting SPOM and excreting the material that is not nutritionally valuable. In Pennak (1953), the diet of Pelecypoda (now Bivalvia) is described as consisting of zooplankton, phytoplankton, and organic detritus. This suspended material is removed from the water and the inorganic silt is separated out, possibly via the labial palps. Therefore, only a portion of the ingested material is actually getting assimilated into their tissues. A study by Grey *et al.* (2001) showed that the $\delta^{15}N$ and $\delta^{13}C$ values of POM were higher than the values for phytoplankton. This may explain why my bivalve samples had stable isotope values higher than that of the SPOM samples.

It is also possible that SPOM could be variable within the wetland itself and my six-sample composite was not representative of the SPOM throughout the sample site. Wave action could be stirring up other material from within the wetland, such as detritus or loosely attached algae. There are many variables here and unfortunately no clear solution without knowing the composition of the SPOM samples which were completely consumed for the stable isotope analysis.

There is also some debate about the feeding behavior of bivalves. Allen (1914) indicated that bivalves are clearly selective feeders, rejecting harmful material and ingesting mostly material with higher food value. The observations

of Gale and Lowe (1971) suggest that *S. transversum* (Sphaeriidae) are non-selective and in most instances, their gut contents reflected the phytoplankton in the water.

There are two types of feeding for bivalves, suspension and deposit. Suspension feeding is the consumption of particles from the water column and deposit feeding is the removal of particles from the sediment (Raikow and Hamilton 2001). A study by Raikow and Hamilton (2001) showed that the diet of *Sphaerium striatinum* consisted of 64% episammon (detritus and algae possibly mixed with sand collected from the surface of sand deposits), and 36% suspended particulate organic matter. Deposit feeding or resuspension may be a contributor to the diet of fingernail clams (Vaughn and Hakenkamp 2001). This idea is also supported in a study by Way (1989) where he observed that *Musculium transversum* could move material using ciliary tracts on the foot and they could also direct their siphons to consume substrate with a "vacuuming motion." With this in mind, the fingernail clams I studied may have a mixed diet consisting of SPOM and fine benthic organic material.

Gastropods are scrapers and I expected a diet consistent with that functional feeding group. I did not see this relationship for the periphyton samples that I collected. Therefore, there must be another food source not accounted for in this study. Detritus could play a much larger role in macroinvertebrate diet than originally predicted. Detritus was not analyzed because of the anticipated difficulty in obtaining a clear isotopic signature. Typically organisms that feed on detritus are actually utilizing it for the colonized

microorganisms, not the decaying material itself. Cummins (1974) describes this as the "peanut butter" on the "nutritionally unsuitable cracker." To get to the "peanut butter," the "cracker" must also be consumed. Similarly, the layer of microorganisms is difficult to sample without including its substrate and therefore was not included in this study.

Although snails are considered nonselective feeders, there is evidence that they may not be consuming all available food. A study by McCormick and Stevenson (1989) showed that when snails fed on periphyton, algal size and growth form were important in the grazing of food. Algae with a more prostrate growth form were removed less readily than other algal species. A subsequent study by Tuchman and Stevenson (1991) showed that a snail grazer removed the overstory filamentous cyanobacteria, leaving lower profile species that are difficult to remove. These different layers of epiphyton may have different stable isotope signatures. A study by Burkholder *et al.* (1990) demonstrated that the adnate taxa from their periphyton community obtained more nutrients from its substrate compared to the loosely attached algae that obtained nutrients from the water column. I did not sample understory and overstory periphyton separately, so I cannot evaluate this source of variability. Another variable discussed later is the variability in periphyton stable isotope signatures at the site level (Figure 15).

As mentioned before, amphipods can consume and assimilate detritus, filamentous algae, and animal material (Summers *et al.* 1997). Pennak (1953) describes amphipods as mainly feeding on plant and animal matter and those found within vegetation as often "browsing on the film of microscopic plants,

animals, and organic debris covering the leaves and stems." Waldbauer (1968) refers to the amphipod *Gammarus* spp. as a "facultative shredder," predicting that when certain food resources are limited, they can shift their diet (Cummins and Klug 1979). This may result in reduced efficiency of food conversion to growth, but *Gammarus* spp. can utilize coarse particulate organic matter (CPOM), FPOM or ultrafine particulate organic matter (UPOM), sediment FPOM-UPOM, periphyton, or invertebrate prey in stream ecosystems. In this study, I did not find that amphipods were feeding on periphyton or SPOM. Because amphipods are primarily shredders, they are likely consuming CPOM, which was not analyzed due to anticipated difficulty in obtaining a clear isotopic signature for this material.

I also examined the stable isotope signatures for mayflies (family: Caenidae), which could reflect SPOM, FPOM, periphyton, or detritus (Merritt and Cummins 1996). A study by Pupilli and Puig (2003) looked at the effects of a major disturbance on mayflies. Before and after a flood, detritus was the major component of their diet. Chessman (1986) conducted a study of the digestive tract contents for caenid mayflies and found 90% ultrafine detritus and 10% benthic algae. A diet primarily consisting of detritus was also supported by a study of snag-dwelling mayflies where greater than 70% of mayfly production was attributed to amorphous detritus and about 18% was based on diatom consumption (Benke and Jacobi 1994). The results of my study are consistent with these other studies, indicating that caenid mayflies were not consuming

SPOM or periphyton as their major food source, suggesting that they are likely consuming FPOM or detritus.

Nutrient loading to aquatic systems has been shown to increase primary production (Wetzel 2001). I had hypothesized that the wetlands with higher nutrient concentrations would have a food web more based on phytoplankton production. Without establishing clear producer-consumer relationships, I am unable to make any inferences about the base of the food webs that were studied. In forested stream systems, detritus has also been shown to be the major source of nutrition for consumers (Hall *et al.* 2001). When eutrophication occurs, detrital biomass increases as well as algal production. This is because there is greater net primary production until shading promotes the breakdown of light-deprived macrophytes, thus contributing to the detrital pool. A study by Keuogh *et al.* (1996) established phytoplankton as the base of the food webs of both coastal wetland and adjacent offshore waters of Lake Superior, but hypothesized that the decomposition of detritus contributed to the $\delta^{13}C$ value of the phytoplankton. This is due to the respiration of the detritus, thus releasing dissolved inorganic carbon that is depleted in ^{13}C, resulting in phytoplankton depleted in ^{13}C. This suggests that despite which source of carbon was identified as the base of the food web, all sources of production influence the isotopic composition of consumers, either directly or indirectly.

The final objective of this study was to assess the variability in isotopic signatures of periphyton within a site and evaluate the importance of that source of variability for evaluating food web structure. I collected periphyton from a

number of different plant substrates and found that their stable isotopic signatures varied greatly (Figure 15). This impacts my results in that I chose *Nuphar* spp. and *Nymphea* spp. as host plants for the periphyton component of the diet analysis portion of this study. Due to the high variability in signatures, I may be falsely excluding periphyton as a potential food source. A study by Cornelisen *et al.* (2007) showed that irradiance affects plant $\delta^{15}N$ and $\delta^{13}C$ values. The same plant species collected from different light regimes had varying stable isotope signatures. Another study has shown that there is a high degree of variability in the isotopic signatures of different plant species within the same wetland (Boon and Bunn 1994). Pip and Robinson (1984) showed that differences in algal periphyton compositions exist on different host macrophytes within the same site. All of these studies show that the composition and isotopic signatures of wetland plants and periphyton are highly variable. This is important to consider before excluding periphyton as a potential food source for the consumers studied. In addition to spatial variability, temporal variability is also likely to be important. The stable isotope ratios of microalgae vary over time while consumers integrate this variation to different degrees depending on their growth and turnover because different instars of insect larvae have varying diets based on their size and functional feeding group (Basaguren 2002).

Lacustrine wetlands are dynamic ecosystems that are important for a number of lake and wetland organisms. I was able to show that land use increases TN and TP concentrations and the $\delta^{15}N$ values of wetland biota. I was unable to establish clear relationships between the primary producers and

primary consumers chosen for this study. Food web studies utilizing stable isotope analyses are difficult to conduct due to spatial and temporal variability of consumers and producers and the variability in consumer feeding modes. These are all important concepts to consider when studying aquatic food webs.

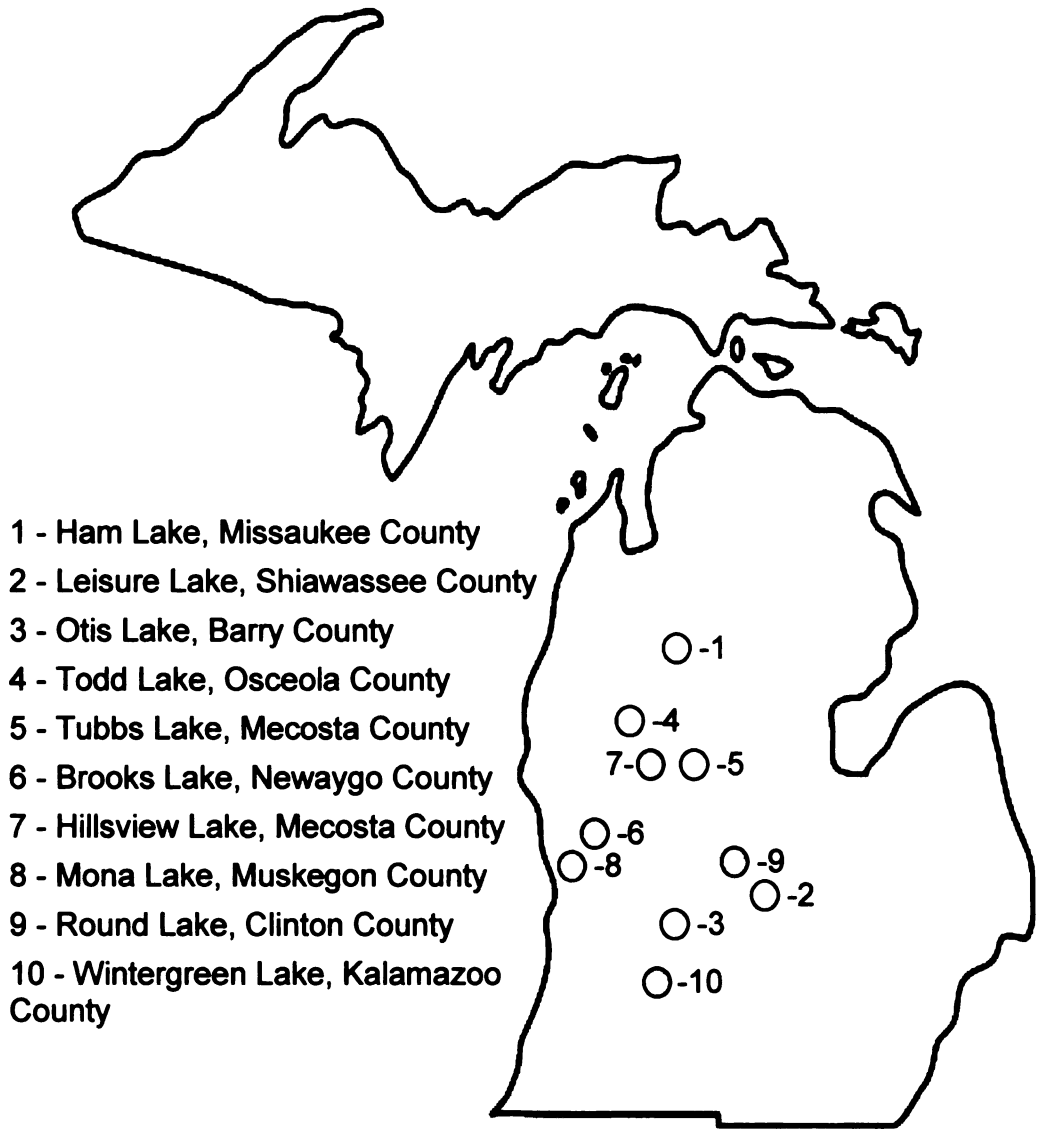
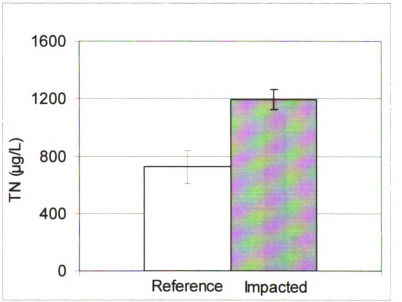


Figure 1. Michigan map of reference sites (white circles) and impacted sites (shaded circles).

(a) Total Nitrogen



(b) Total Phosphorus

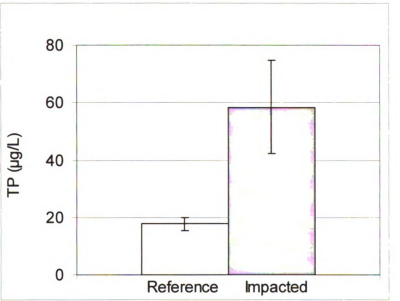


Figure 2. (a) Mean total nitrogen (TN) (µg/L) and (b) mean total phosphorus (TP) (µg/L) for reference (white) and impacted (shaded) sites (error bars are +/- 1 standard error).

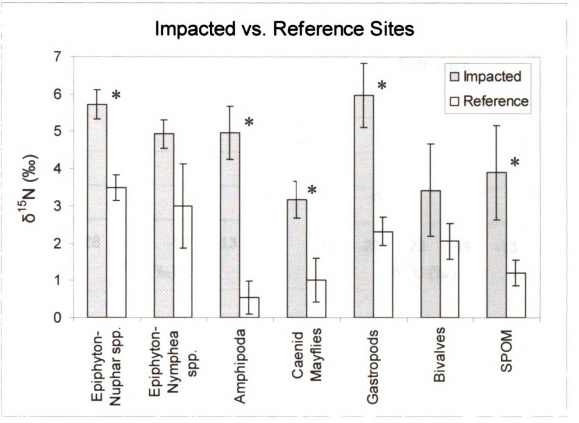


Figure 3. Plot of average $\delta^{15}N$ (‰) values for each set of biota for reference (white) and impacted (shaded) sites (error bars are +/- 1 standard error). Means with * are significantly different ($P<0.05$).

Reference Sites

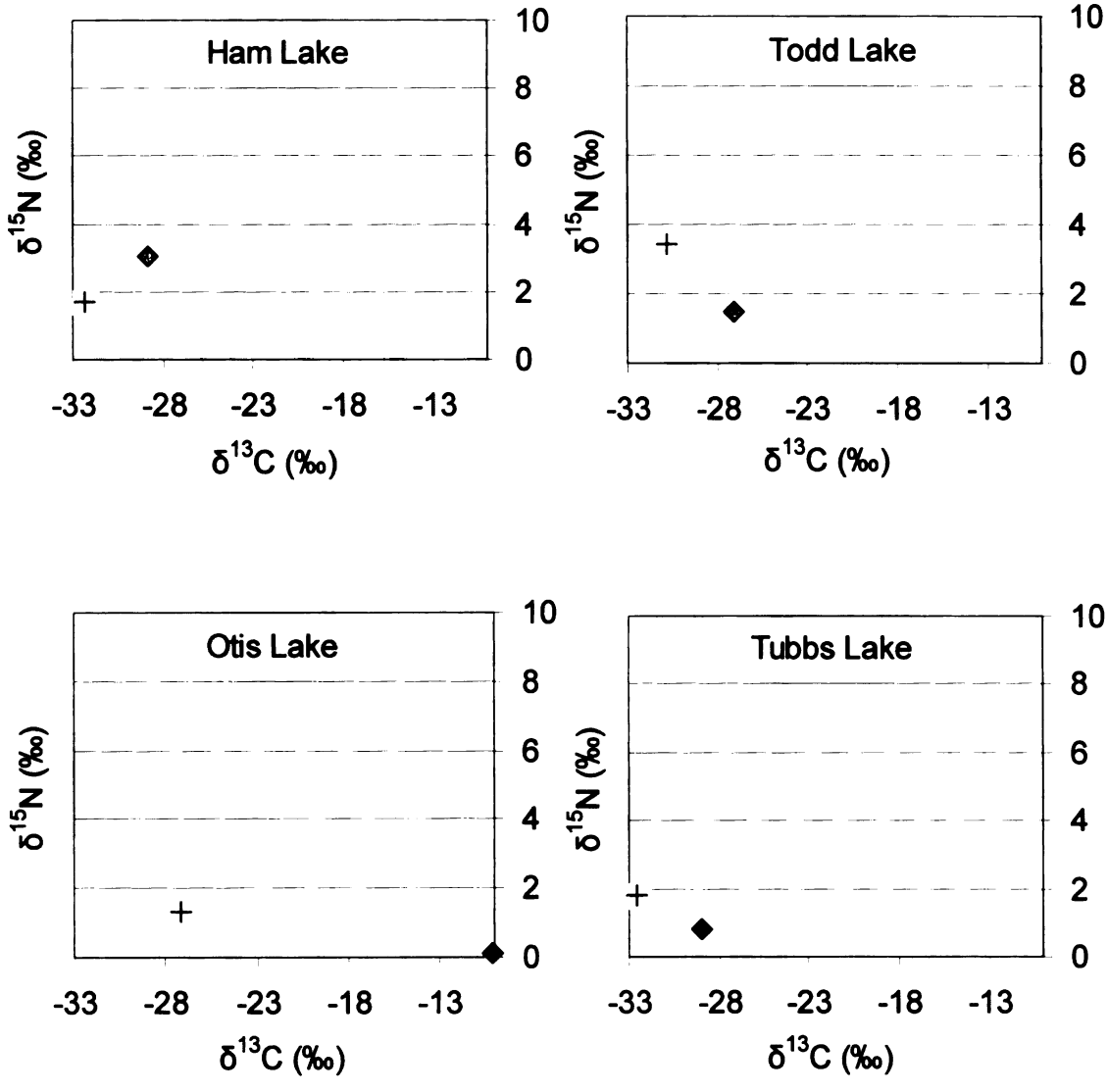


Figure 4. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) for SPOM (shaded diamonds) and bivalves (plus sign) for reference sites.

Impacted Sites

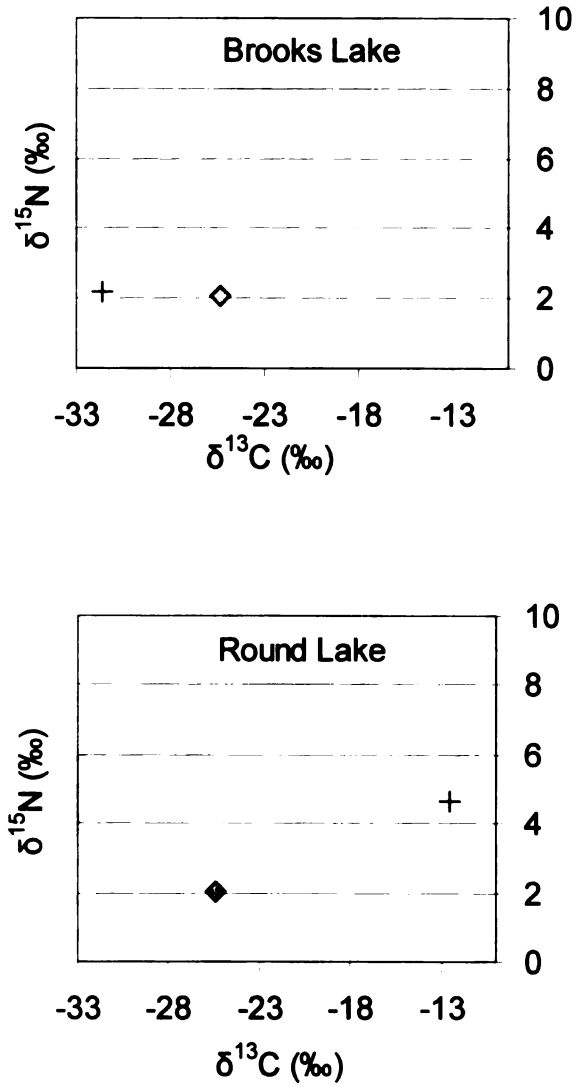


Figure 5. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) for SPOM (shaded diamonds) and bivalves (plus sign) for impacted sites.

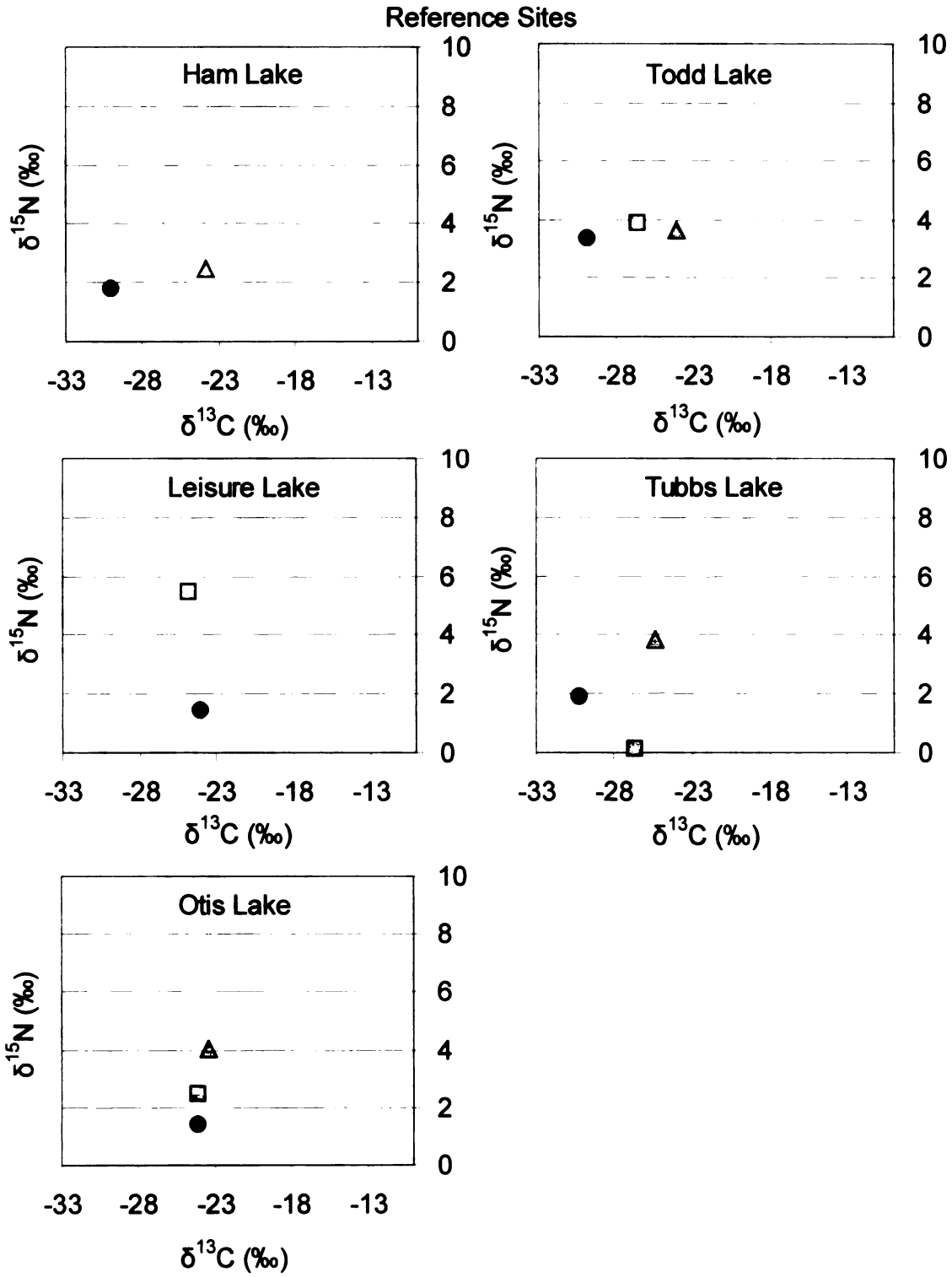


Figure 6. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) of epiphyton from *Nuphar* spp. stems (shaded triangles), epiphyton from *Nymphea* spp. stems (shaded squares), and gastropods (black circles) for reference sites.

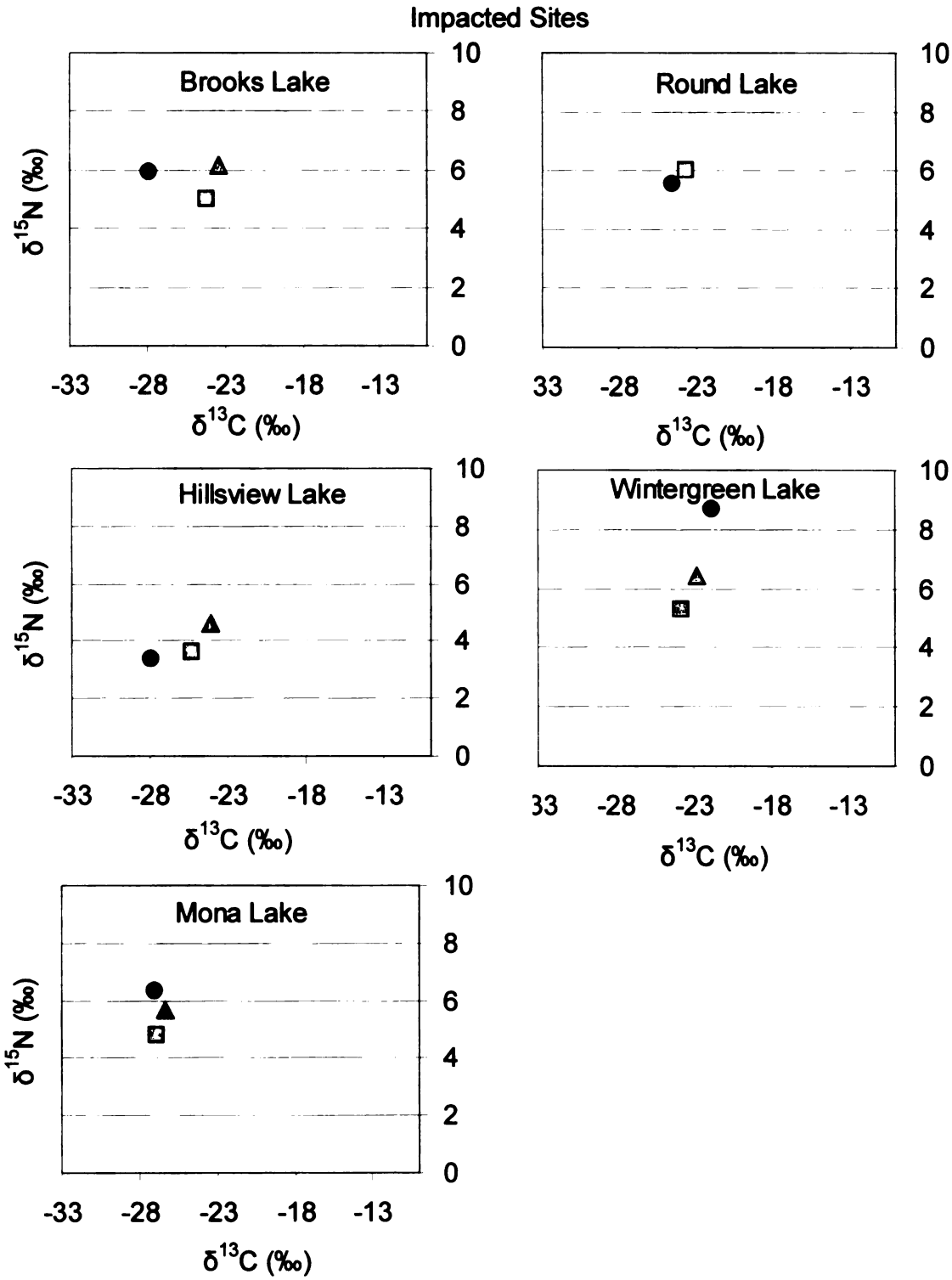


Figure 7. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) of epiphyton from *Nuphar* spp. stems (shaded triangles), epiphyton from *Nymphea* spp. stems (shaded squares), and gastropods (black circles) for impacted sites.

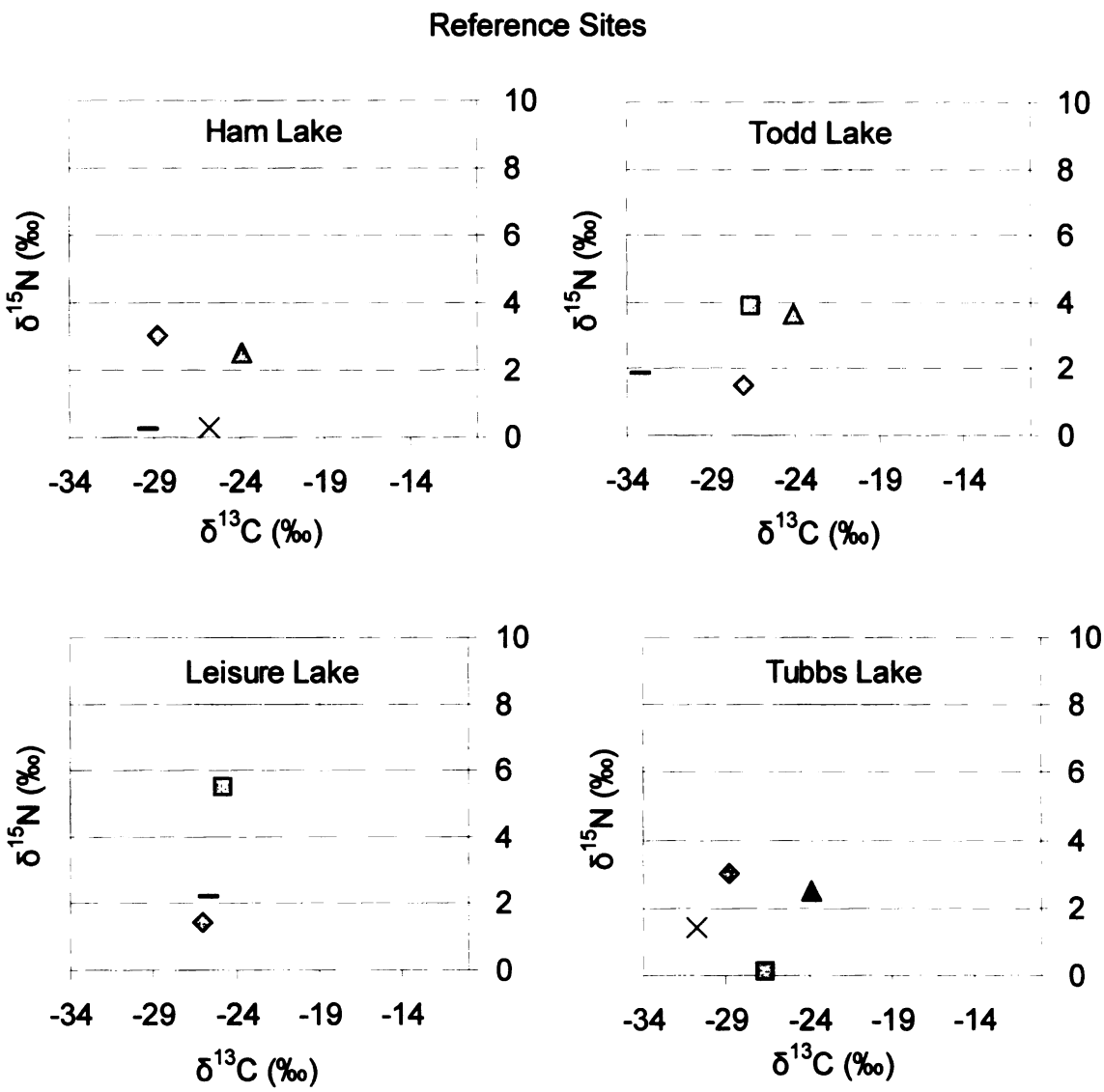


Figure 8. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) of epiphyton from *Nuphar* spp. stems (shaded triangles), epiphyton from *Nymphea* spp. stems (shaded squares), SPOM (shaded diamonds), amphipods ("X"s), and mayflies (dashes) for reference sites.

Impacted Sites

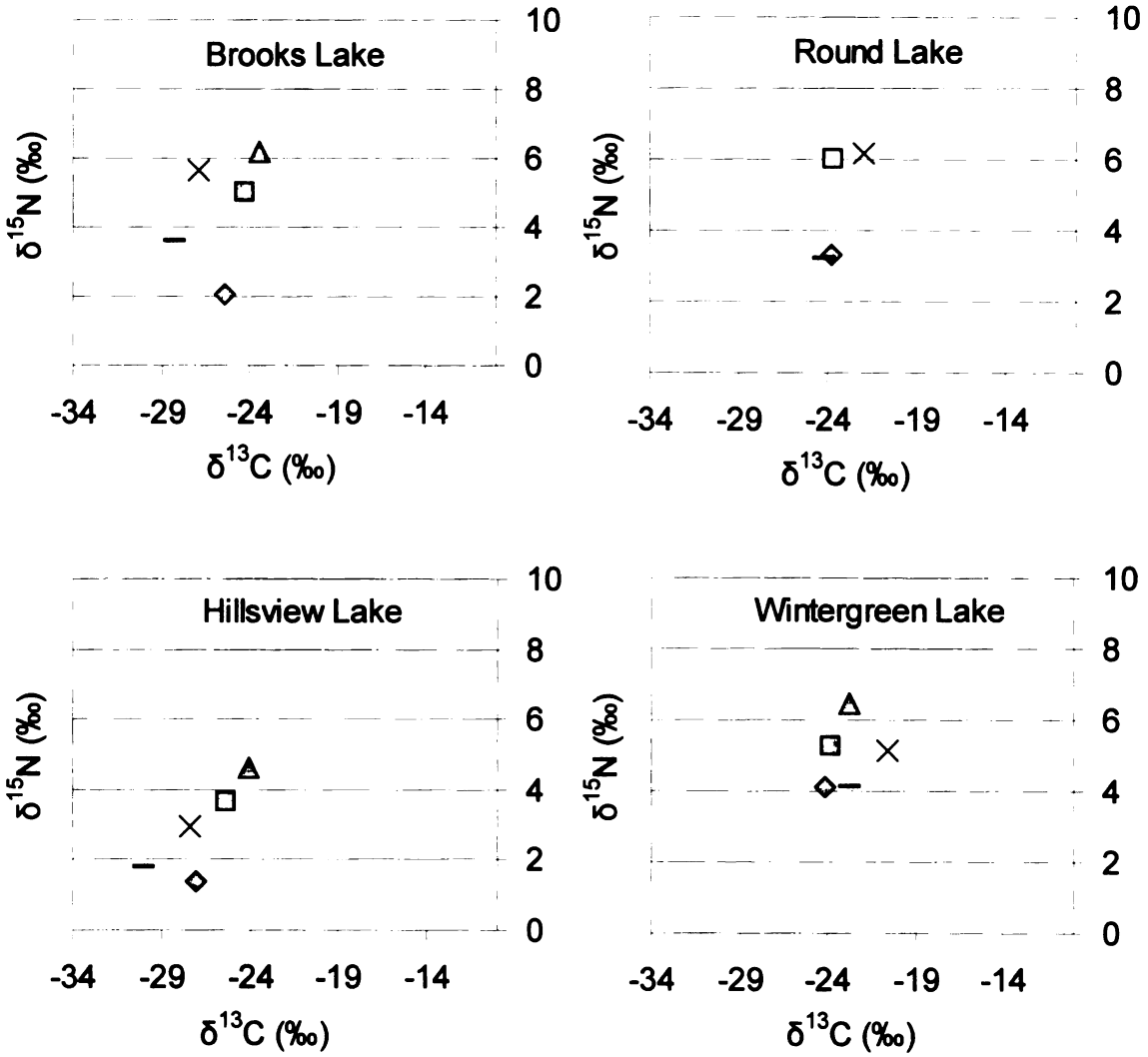


Figure 9. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) of epiphyton from *Nuphar* spp. stems (shaded triangles), epiphyton from *Nymphea* spp. stems (shaded squares), SPOM (shaded diamonds), amphipods ("X"s), and mayflies (dashes) for reference sites.

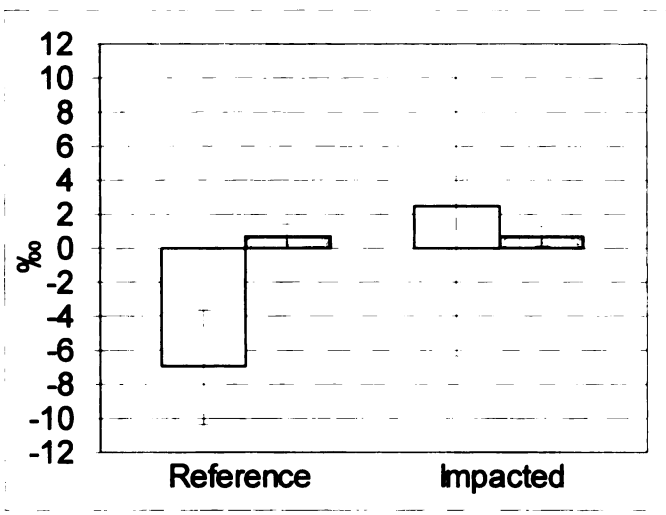
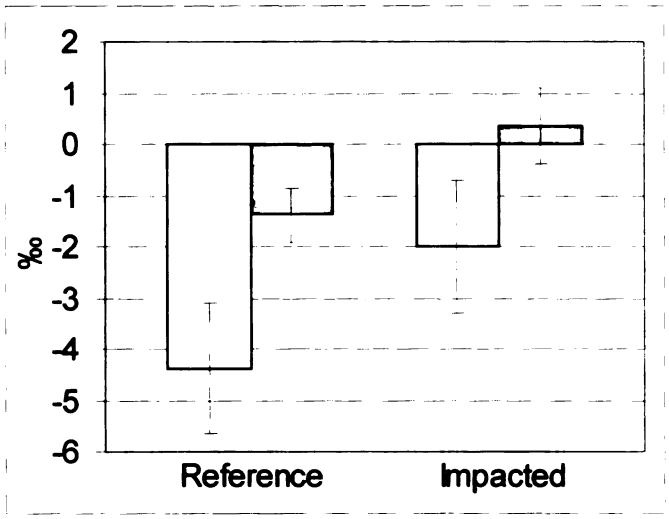


Figure 10. Mean difference in $\delta^{13}C$ (white) and $\delta^{15}N$ (shaded) between SPOM and bivalves for reference sites and impacted sites (error bars are +/- 1 standard error).

(a) Epiphyton (*Nuphar* spp.) and Gastropods



(b) Epiphyton (*Nymphea* spp.) and Gastropods

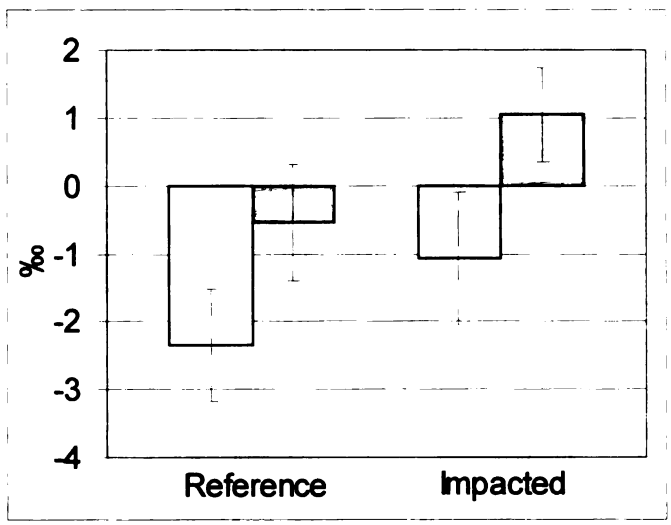
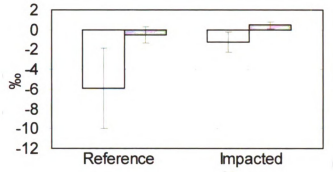
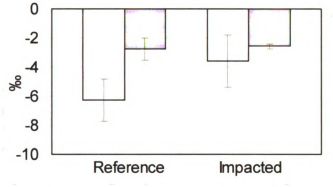


Figure 11. Mean difference in $\delta^{13}C$ (white) and $\delta^{15}N$ (shaded) between (a) epiphyton (*Nuphar* spp.) and gastropods and (b) epiphyton (*Nymphea* spp.) and gastropods for reference sites and impacted sites (error bars are +/- 1 standard error).

(a) SPOM and Caenid Mayflies



(b) Epiphyton (*Nuphar* spp.) and Caenid Mayflies



(c) Epiphyton (*Nymphea* spp.) and Caenid Mayflies

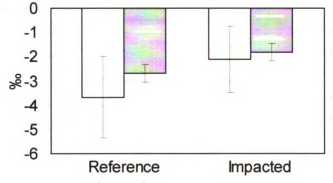
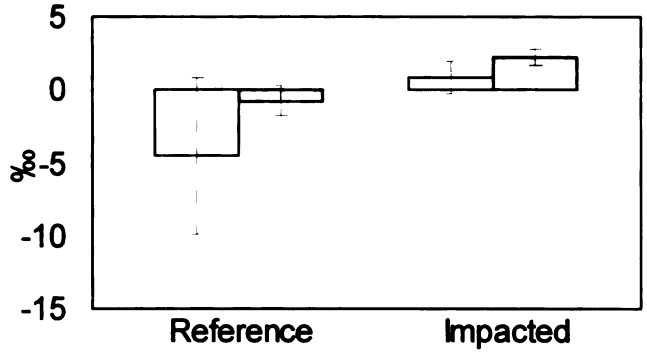
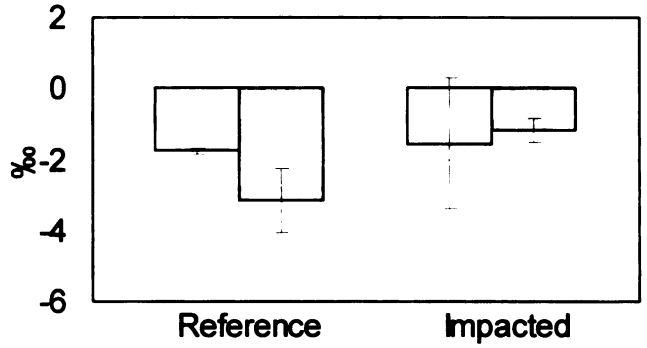


Figure 12. Mean difference in $\delta^{13}C$ (white) and $\delta^{15}N$ (shaded) between (a) SPOM and caenid mayflies, (b) epiphyton (*Nuphar* spp.) and caenid mayflies, and (c) epiphyton (*Nymphea* spp.) and caenid mayflies for reference sites and impacted sites (error bars are +/- 1 standard error).

(a) SPOM and Amphipods



(b) Epiphyton (*Nuphar* spp.) and Amphipods



(c) Epiphyton (*Nymphea* spp.) and Amphipods

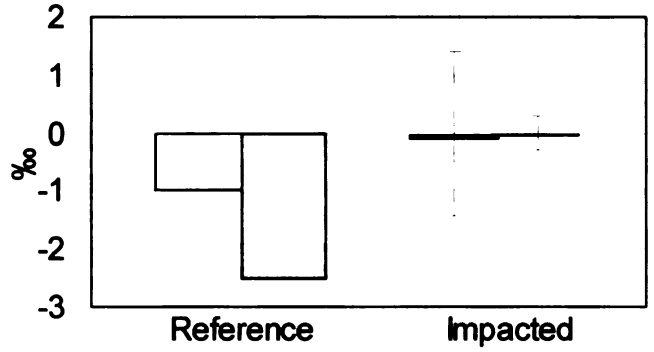


Figure 13. Mean difference in $\delta^{13}C$ (white) and $\delta^{15}N$ (shaded) between (a) SPOM and amphipods, (b) epiphyton (*Nuphar* spp.) and amphipods, and (c) epiphyton (*Nymphea* spp.) and amphipods for reference sites and impacted sites (error bars are +/- 1 standard error).

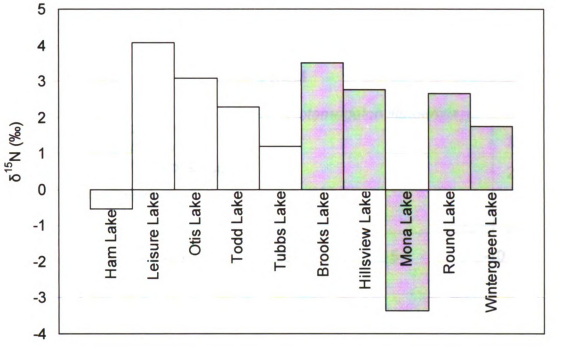
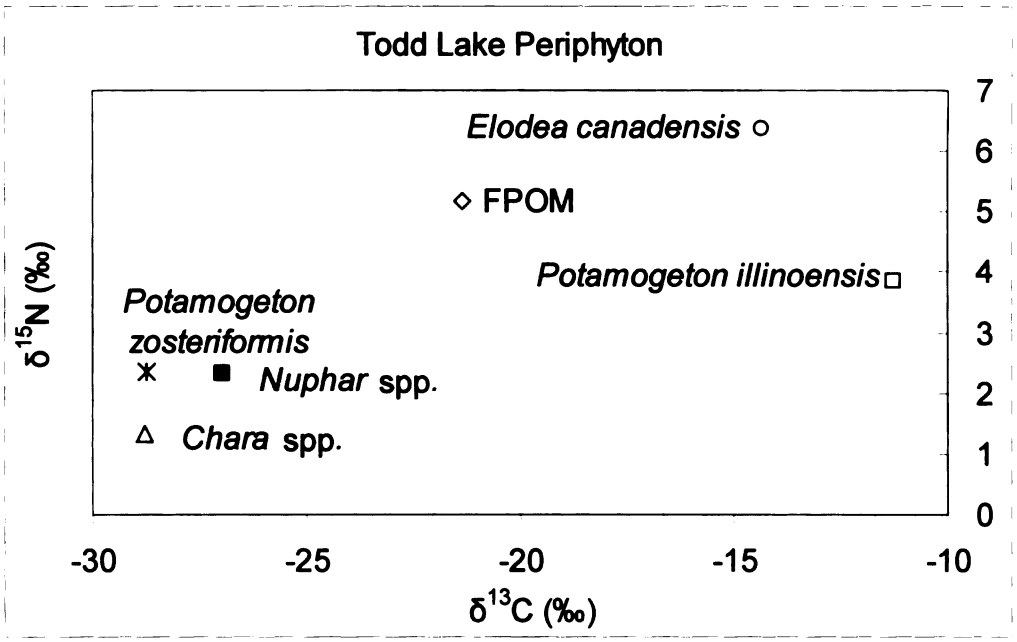


Figure 14. Difference in $\delta^{15}N$ between SPOM and epiphyton (averaged from *Nuphar* spp. and *Nymphea* spp.) for reference sites (white) and impacted sites (shaded).

(a)



(b)

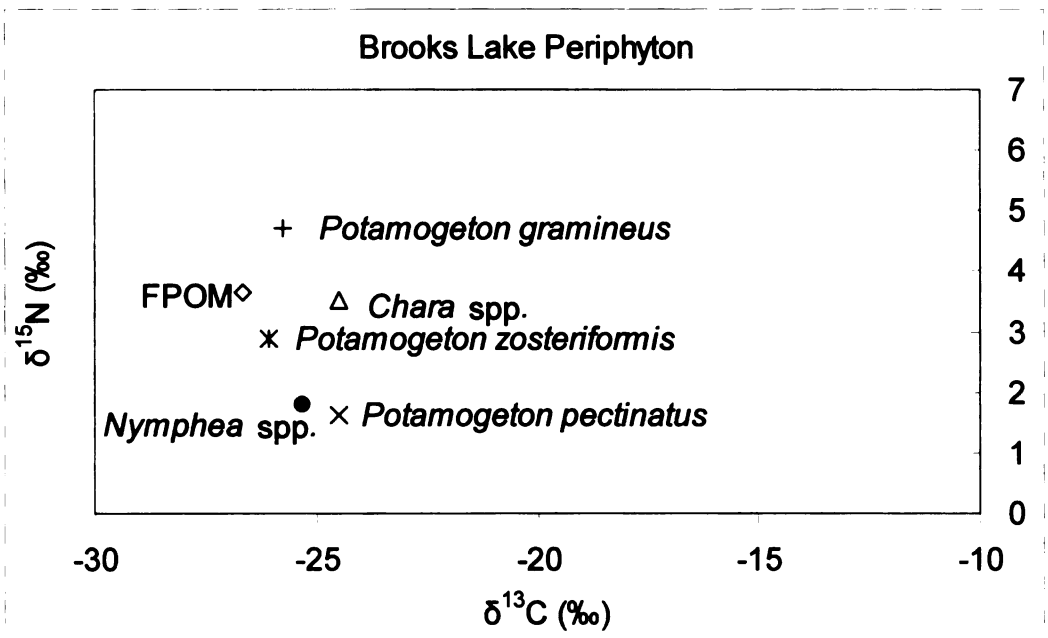


Figure 15. $\delta^{15}N$ (‰) vs $\delta^{13}C$ (‰) for FPOM and periphyton collected off of different substrates for (a) Todd Lake (reference site) and (b) Brooks Lake (impacted site).

APPENDIX

Wetland Site Michigan County *Samples collected July 2003	Ham Lake Missaukee	Leisure Lake Shiawassee	Otis Lake Barry	Todd Lake Osceola	Tubbs Lake Mecosta	Brooks Lake Newaygo	Hillsview Lake Mecosta	Mona Lake Muskegon	Round Lake Clinton	Wintergreen Lake Kalamazoo
Latitude (°N)	44.50	42.82	42.61	43.95	43.71	43.39	43.71	43.18	42.88	42.40
Longitude (°W)	85.26	84.35	85.41	85.45	85.21	85.75	85.37	86.22	84.44	85.38
Total Nitrogen (µg/L)	435	950	1047	540	646	1083	1200	1441	1232	1019
Total Phosphorus (µg/L)	9.3	19.0	17.6	23.3	19.1	34.3	119.2	64.0	38.7	36.2

Table 1. Site information including Michigan county, latitude, longitude, total nitrogen (µg/L), and total phosphorus (µg/L).

Wetland Site Michigan County *Samples collected July 2003	Ham Lake Missaukee	Leisure Lake Shiawassee	Otis Lake Barry	Todd Lake Osceola	Tubbs Lake Mecosta	Brooks Lake Newaygo	Hillsview Lake Mecosta	Mona Lake Muskegon	Round Lake Clinton	Wintergreen Lake Kalamazoo
Stable Isotope Data $\delta^{15}N$ (‰)										
▪ SPOM	3.03	1.43	0.13	1.48	0.79	2.06	1.39	8.59	3.37	4.10
▪ Epiphyton–*Nuphar* spp.	2.49		4.04	3.63	3.83	6.16	4.64	5.67		6.43
▪ Epiphyton–*Nymphea* spp.		5.49	2.46	3.88	0.14	4.98	3.64	4.77	5.99	5.29
▪ Amphipoda	0.26				1.40	5.66	2.93		6.18	5.12
▪ Caenid Mayflies	0.21	2.18		1.83		3.58	1.78		3.18	4.12
▪ Bivalves	1.68		1.31	3.45	1.78	2.18			4.67	
▪ Gastropods	1.79	3.11	1.44	3.33	1.90	5.91	3.36	6.36	5.54	8.69
Stable Isotope Data $\delta^{13}C$ (‰)										
▪ SPOM	-28.84	-26.07	-10.15	-27.12	-28.96	-25.36	-27.02	-26.09	-23.79	-24.14
▪ Epiphyton–*Nuphar* spp.	-23.89		-23.37	-24.07	-25.30	-23.43	-24.09	-26.41		-22.73
▪ Epiphyton–*Nymphea* spp.		-24.80	-24.10	-26.57	-26.64	-24.19	-25.26	-26.94	-23.63	-23.75
▪ Amphipoda	-25.72		-25.07		-30.79	-26.86	-27.43		-21.94	-20.62
▪ Caenid Mayflies	-29.38	2.18	-27.58	-33.20		-28.32	-29.95		-24.25	-22.80
▪ Bivalves	-32.40		-27.20	-30.81	-32.53	-31.66			-12.50	
▪ Gastropods	-30.07	-27.42	-24.05	-29.82	-30.21	-27.89	-27.91	-27.03	-24.50	-21.81

Table 2. $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) values for each site for suspended particulate organic matter (SPOM), Epiphyton-*Nuphar* spp., Epiphyton-*Nymphea* spp., amphipods, caenid mayflies, bivalves, and gastropods, where present.

Wetland Site Michigan County *Samples collected July 2003	Ham Lake Missaukee	Leisure Lake Shiawassee	Otis Lake Barry	Todd Lake Osceola	Tubbs Lake Mecosta	Brooks Lake Newaygo	Hillsview Lake Mecosta	Mona Lake Muskegon	Round Lake Clinton	Wintergreen Lake Kalamazoo
Bivalve Presence (Family)										
▪ Sphaeriidae	x		x	x	x	x			x	
Gastropod Presence (Family)										
▪ Lymnaeidae				x	x	x		x		
▪ Physidae	x	x	x			x	x	x	x	x
▪ Planorbidae	x	x		x	x		x			
▪ Viviparidae			x							

Table 3. Bivalve and gastropod family presence for each site. Presence is represented by and "x."

Wetland Site County *Samples collected in August 2004	Todd Lake Osceola	Brooks Lake Newaygo
Stable isotope data of $\delta^{15}N$ (‰) collected from the following substrata:		
▪ FPOM	5.18	3.65
▪ *Chara* spp.	1.33	3.51
▪ *Elodea canadensis*	6.36	
▪ *Nuphar* spp.	2.33	
▪ *Nymphea* spp.		1.79
▪ *Potamogeton gramineus*		4.71
▪ *Potamogeton illinoensis*	3.86	
▪ *Potamogeton pectinatus*		1.61
▪ *Potamogeton zosteriformis*	2.35	2.89
Stable Isotope Data $\delta^{13}C$ (‰) collected from the following substrata:		
▪ FPOM	-21.35	-26.68
▪ *Chara* spp.	-28.78	-25.17
▪ *Elodea canadensis*	-14.33	
▪ *Nuphar* spp.	-26.95	
▪ *Nymphea* spp.		-25.29
▪ *Potamogeton gramineus*		-25.77
▪ *Potamogeton illinoensis*	-11.28	
▪ *Potamogeton pectinatus*		-24.50
▪ *Potamogeton zosteriformis*	-28.74	-26.09

Table 4. $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) values for epiphyton collected from the indicated plant substrata and fine particulate organic matter (FPOM) from the sediment surface, where present.

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