USING COARSE-SCALE PHYSICAL LAKE CHARACTERISTICS TO MODEL LAKE STURGEON (*Acipenser fulvescens*) FEEDING HABITAT AND THEIR PREY

by

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A graduate thesis submitted
in partial fulfillment of the requirements for
The degree of Masters of Science in Forestry

Faculty of Natural Resources Management
Lakehead University

May 7, 2012

SUMMARY

Lebron, M.M. 2012. A simplified model for a lake ecosystem using coarse-scale physical lake characteristics: Lake sturgeon (*Acipenser fulvescens*) feeding habitat and their prey. Lakehead University. 39 pp.

Coarse-scale, physical lake characteristics (lake fetch, shoreline exposure, and littoral-zone slope) were investigated as to their ability to predict benthic macroinvertebrate communities and lake sturgeon feeding along shorelines in the southern portion of Rainy Lake. Rainy Lake is a large water body and hosts a fishery shared between Minnesota, U.S.A. and Ontario, Canada. Benthic samples were drawn from different sections of the littoral zone during a period of three months in the summer of 2010 and in August 2011. The biomass (mg/m^2) of eight individual taxa and total biomass across 12 macroinvertebrate taxa were measured and monitored over the first season and used to characterize lake sturgeon (*Acipenser fulvescens*) feeding habitat with a best-fit model of the physical lake characteristics, including the effect of season on biomass. Shoreline reaches were considered to be better feeding habitat if they held greater biomass of preferred food items.

Nonmetric multidimensional scaling of the physical variables and an information-theoretic approach to general linear modeling of were used to support the conclusion that shoreline reaches with short fetch (< 1 km across water) supported greater biomass of bivalves (Class: Bivalvia), caddisflies (Class: Insecta; Order: Trichoptera) and dragonflies (Suborder: Anisoptera), while long fetches (> 2 km across water) were characteristic of greater snail (Class: Gastropoda) biomass. During July and August greater total biomass, as well as greater biomass of snails and crayfish (Order: Decapoda), occurred on steep littoral-zone slopes (> 11.3˚), while biomass of bivalves was greater on gentle littoral-zone slopes (< 8.5˚) during the same season. Mayfly (Class: Insecta; Order: Ephemeroptera) biomass could not be predicted by the best-fit model, but shoreline reaches with short fetches and gentle littoral-zone slopes were likely their preferred habitat. Mayflies experienced a large decline in biomass from June to July, suggesting that lake sturgeon could feed most efficiently if they selected exposed shorelines (angle of exposure > 100˚) with short fetch during June and then switched to exposed shorelines with long fetch and steep littoral-zone slopes during July and August.

Random sections of shoreline were sampled in 2011 to confirm the association between short fetch with greater biomass of bivalves and caddisflies and the association of gentle littoral-zone slopes with greater biomass of bivalves. Additionally, 2011 data showed lower biomass of mayflies with longer fetch, and lower biomass of bivalves and caddisflies at larger angles of shoreline exposure. Higher biomass of dragonflies and caddisflies, meanwhile, occurred on gentler littoral-zone slopes.

Lake sturgeon locations from radio telemetry were characterized according to fetch, shoreline exposure and slope of the areas surrounding them. These associations were then compared to the best-fit benthic biomass model to test for similarity in the relationships between the coarse-scale, physical lake characteristics and frequency of lake sturgeon locations during July and August 2003-2004. Lake sturgeon used exposed shoreline reaches regardless of fetch; they were more likely to be found on steep littoral-zone slopes in August. Based on macroinvertebrate community biomass and telemetry locations of lake sturgeon during June, July and August, habitat management strategies should consider exposed shoreline reaches and littoral zones that provide greater biomass of preferred prey items as areas of special concern to be protected from development for the conservation of lake sturgeon. This study illustrates how a simplified set of physical lake characteristics can offer predictive information about a complex lake ecosystem.

Key Words: *Acipenser fulvescens,* benthic macroinvertebrates, habitat suitability models, lake sturgeon feeding, limnology, littoral zone, Rainy Lake, Voyageurs National Park.

CONTENTS

ACKNOWLEDGMENTS

This thesis would not have been possible without the support of many people and establishments. Foremost, I would like to thank Dr. Brian McLaren, my thesis advisor, for providing a laptop, outboard motor and his time, dedication and knowledge. My other committee members, Dr. Steve Windels and Dr. Rob Mackereth provided very useful knowledge and direction to this project. Funding from Lakehead University’s Faculty of Natural Resources Management, NSERC Discovery, Rainy Lake Fisheries Charity Trust and Voyageurs National Park allowed my schooling and fieldwork to be possible. Voyageurs National Park also provided wonderful field camp locations on Rainy Lake and some needed gear to carry out the fieldwork. I also want to thank my five field assistants, Ben Kuchta, Kyle Myschowoda, Stephen Kwiatkowski, Florian Ruerink, and Andrea Cranston. Lastly, thank you, Dr. Steve Chipps, for putting my thesis through the final stage of review.

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INTRODUCTION

Recent interest in lake sturgeon (*Acipenser fulvescens*) is due to the current state of populations in areas of the U.S.A. and Canada where historic populations once thrived. In various provinces and states lake sturgeon populations are considered extirpated, endangered, threatened, or of special concern (COSEWIC 2006; Holey and Trudeau 2005; Leonard et al. 2004). Much of the research involving lake sturgeon has been related to year-class strength, migration routes, and habitat suitability models (HSMs) for feeding and spawning in specific populations. The HSMs have primarily been used for classification of habitat in river (lotic) systems and are rarely applied to lake (lentic) systems; they have been based on water depth, substrate type and water velocity (Threader et al. 1998). For lentic systems, similar variables might be chosen for feeding HSMs based on how they influence concentrations of invertebrates important to the lake sturgeon diet.

Lake sturgeon are bottom feeders that prey on benthic macroinvertebrates, such as insect larvae (Class: Insecta), leeches (Class: Clitellata; Subclass: Hirudinea), crayfish (Class: Malacostraca; Order: Decapoda) and mollusks (Phylum: Mollusca; Peterson et al. 2007). Physical, chemical and biological factors play a role in creating a range of horizontal and vertical variation in lentic environments that create niches for different types of invertebrates (Covich et al. 1999). Rainy Lake, a shared water body between Minnesota (U.S.A.) and Ontario (Canada), and habitat for a lake sturgeon population for which baseline information has recently become available (Adams et al. 2006a), is the focus of this study, which evaluates shoreline invertebrate community structure and biomass against coarse-scale, physical lake characteristics in the context of summer feeding by lake sturgeon. The characteristics explored here include littoral slope, angle of exposure to wind and waves, and fetch in the prevailing northwest and southeast wind directions.

Use of coarse-scale, physical lake characteristics to evaluate lake sturgeon habitat in relationship to their diet depends on a few key assumptions. The first assumption is that the value of lake sturgeon feeding areas can be characterized by composition and biomass of their prey community. Secondly, an assumption is that food habits on Rainy Lake are similar to those investigated in nearby Lake of the Woods and in Rainy River, where the only regional diet data exists (Mosindy and Rusak 1991). Another assumption is that lake sturgeon summer feeding occurs mainly in the littoral zone of Rainy Lake, as previously determined from radiotelemetry (Adams et al. 2006b). The associated location dataset will be used to compare predictions of prey biomass derived from lake characteristics to locations of 41 monitored lake sturgeon during June-August, 2003-2004. A final assumption is that the same feeding areas are used year to year by lake sturgeon and will correspond to the prey communities investigated in 2010 and 2011.

CONTEXT

Lake sturgeon are native to the major drainages in North America, including the Mississippi River, the Great Lakes, and Hudson Bay (Peterson et al. 2007). Most lake sturgeon populations have been reduced by overfishing, habitat degradation and artificial barriers to migration (Manny and Kennedy 2002). Lake sturgeon use a range of habitat types throughout their life, migrating to different areas for spawning or feeding as juveniles and adults (Werner and Hayes 2006). Literature pertaining to the species has mainly focused on lotic systems where lake sturgeon spawn, often a response to management concerns on the potential impact of streamside habitat degradation and barriers to migration created by the installation of hydroelectric dams. Identifying the lentic habitat requirements for adult feeding is also important for habitat restoration and the long-term conservation of lake sturgeon. With the results of research steered toward examining invertebrate communities as they relate to different shoreline types, it will be easier to draw inferences on how lake-level fluctuations might disrupt invertebrate prey communities or to identify and protect critical habitat from recreational harvest. Decisions on lakefront development may also benefit from knowledge of the invertebrate community and act toward the long-term conservation of lake sturgeon feeding habitat.

Classification systems for sturgeon habitat have already been developed, with the most common method being HSMs. HSMs have been used to manage species of special concern, but were developed largely though expert opinion rather than through empirical studies. Haxton et al. (2008) validated a HSM developed for predicting lake sturgeon feeding habitat in northern rivers of Ontario. The validated HSM used bottom substrate, water depth and water velocity, which predicted the distribution and abundance of lake sturgeon in lotic feeding habitats. The current study investigates how macroinvertebrate communities vary in structure and abundance along different shoreline reaches and how this variation might influence lake sturgeon feeding in lentic ecosystems. Eight shoreline classifications were chosen by examining lake charts and from eight combinations of fetch, littoral-zone slope and exposure to open water. An overall goal was to evaluate how well lake sturgeon feeding habitat might be characterized by coarse-scale, physical lake characteristics, which does not require field sampling. Substrate type and macrophyte coverage were also recorded in this study due to their importance in explaining finer-scale variation in invertebrate community composition and prey biomass. Ultimately, these two variables were not considered in modeling efforts to predict prey biomass, because, unlike fetch, littoral-zone slope and shoreline exposure, substrate type and macrophyte coverage must be determined on-site.

OBJECTIVES

This study relies on counts and biomass estimates in 2010 and 2011 of 14 taxonomic groups of macroinvertebrates considered as lake sturgeon prey, and on lake sturgeon locations on Rainy Lake collected during June-August, 2003-2004 (Adams et al. 2006b). Five objectives address a goal of matching coarse-scale, physical lake characteristics (fetch, littoral-zone slope and shoreline exposure to open water) to the ecosystem defined by the lake sturgeon and its prey:

1) Determine how benthic sediment types and near-shore macrophyte abundance are associated with fetch, littoral-zone slope and exposure will be described. The prediction is that shorelines with gentle littoral-zone slopes sheltered from the effects of wind and waves will be dominated by finer substrates and a greater abundance of macrophytes, while coarse substrates and absence of macrophytes will characterize shorelines with long fetch, large angles of exposure and steep littoral-zone slopes.

2) To associate variation among macroinvertebrate communities with combinations of fetch, exposure and littoral-zone slope. It is predicted that all three coarse-scale lake characteristics will contribute to defining the habitat of different benthic communities and explaining the distribution of individual macroinvertebrate taxa. This

objective is the most important to predicting lake sturgeon feeding habitat. The physical lake characteristics and various interactions among them will be explored in a set of *a priori* models, of which one will be considered the best-fit in predicting total macroinvertebrate biomass, as well as the biomass of individual taxa in a multivariate model.

3) Monthly changes in biomass will be tracked for macroinvertebrate taxa important to the lake sturgeon diet. Seasonal changes in invertebrate biomass are expected due to larval growth, death, and emigration to different habitats, in particular emergence into the terrestrial environment. This seasonal component will represent an additional variable explored in the set of *a priori* multivariate models defining macroinvertebrate biomass.

4) Test the model predicting macroinvertebrate biomass by sampling shoreline areas in 2011 and comparing significant trends to those found in 2010. We predict that macroinvertebrates will show similar habitat preferences between years.

5) A final objective will be to test whether lake sturgeon use feeding habitat along shoreline reaches that are predicted, according to the best-fit model from Objectives 2 and 3, to have greater biomass of their preferred foods. Lake sturgeon should selectively feed using an optimal foraging strategy (feeding where there is greater biomass of preferred food items) and choose feeding habitat differently through the summer if monthly changes in prey biomass are tracked.

The value of this study lies in its ability to predict, using a simplified set of coarse-scale, physical lake characteristics, elements of a complex ecosystem. It stands not only as a partial validation of the lake sturgeon HSM in the Rainy Lake water body, but also as an example of the use of easily measured lake characteristics in modelling a benthic ecosystem.

LITERATURE REVIEW

Lake sturgeon feeding, benthic communities and lake characteristics

Lake sturgeon are large, prehistoric-looking benthic grazers that feed on macroinvertebrates (Peterson et al. 2007). While feeding, lake sturgeon swim along the bottoms of lakes and rivers with their barbels in contact with substrate. When prey are detected, they are sucked up with a rapid extension of the mouth. The sturgeon jaw is detached from the skull, allowing it to project downward during feeding. The sturgeon barbels are situated close to the tip of the snout, assisting feeding with chemosensory, tactile and electrosensory receptors (Chiasson et al. 1997). Beamish et al. (1998) found that there was no change in prey intake across different adult size classes of lake sturgeon.

The lake sturgeon life cycle is long, with a late onset of maturity (Peterson et al. 2006). Female lake sturgeon may not spawn until age 20 (Auer 1996) and then spawn every subsequent four to nine years, while male lake sturgeon may spawn only every one to three years (Roussow 1957; Magnin 1966; Fortin et al. 1996). Lake sturgeon typically range in size from 15-70 kg, but individuals weighing 145 kg have been recorded (Vecsea and Peterson 2004). Some lake sturgeon individuals use vast areas of habitat. Their home ranges in the South Arm of Rainy Lake have been documented to span from 84 ha to 14,844 ha, with a mean size of 4,625 ha (Adams et al. 2006a). Prey abundance is an important factor in determining habitat selection (Peterson et al. 2007). It is possible that lake sturgeon have large home ranges to compensate for seasonal and regional changes in prey abundance. It is also possible that lake sturgeon compensate for shortages of preferred prey by switching to alternative, less desirable, but more abundant food sources (Beamish et al. 1998). It is also well known that lake sturgeon occupy different habitats to meet all their life history needs, including spawning, feeding and overwintering (Wilson and McKinley 2004).

Prey composition and density is not consistent over the geographical range of lake sturgeon; for this reason, diets vary. From stomach analysis of lake sturgeon taken from the Moose River Basin, northern Ontario, juveniles regularly consume mayflies (Class Insecta; Order: Ephemeroptera), caddisflies (Order: Trichoptera), dragonflies (Suborder: Anisoptera) and leeches (Beamish et al. 1998). In the St. Lawrence River, lake sturgeon smaller than 1 m in length fed mainly on mosquitoes (Order: Diptera; Family: Culicidae) and scuds (Order: Amphipoda), whereas larger individuals fed on mollusks, including snails (Class: Gastropoda), which made up 16.7% of their diet (Werner and Hayes 2005). In Oneida Lake, New York, the main food items for lake sturgeon were scuds, snails and zebra mussels (*Dreissena polymorpha*; Jackson et al. 2002). During an assessment of stomachs from commercially harvested lake sturgeon populations in the Lake of the Woods and Rainy River, crayfish and mayflies (*Hexagenia* spp.) were the most abundant food items (Mosindy and Rusak 1991). Spring mayfly consumption before their emergence proved to be more important to the diet than crayfish consumption. Other diet components of lake sturgeon in Lake of the Woods included bivalves, snails and bloodworms (*Glycera* spp.). This variability in diet supports the idea that lake sturgeon are opportunistic feeders.

Lake sturgeon select feeding areas based on benthic prey abundance (Harkness and Dymond 1961), so benthic prey density and biomass may be used to predict locations with favorable conditions for lake sturgeon feeding. To maximize the rate of energy intake, lake sturgeon likely feed on the largest available prey (Beamish et al. 1998), suggesting that total prey biomass together with its quality is more important than prey quality alone. Keast and Harker (1977) found that many fish concentrate at shallow depths where invertebrate biomass is higher. Concentration in shallow depths provides evidence of greater feeding opportunity to a variety of benthic feeding fish, including the lake sturgeon.

Invertebrate prey present in northern systems have varied habitat preferences. Mayflies commonly occur among littoral-zone vegetation, in relatively deep water and along wind-swept shorelines (Thorp and Covich 1991). A study investigating the impacts of water-level drawdown on invertebrate communities identified seven distinct mayfly species in Voyageurs National Park, each with different habitat use (McEwen and Butler 2008). In contrast, crayfish are generalists, both omnivorous and found in almost all littoral-zone habitats, although typically inhabiting shallow water depths of 1-2 m (Peckarsky et al. 1990). Unlike most of the invertebrate community, which do not succeed on rocky substrates, snails feed on detritus and periphyton on rocky surfaces, cobble and on macrophytes growing in softer substrates; thus, they are also ubiquitous in the littoral zone (Thorp and Covich 1991). Belonging to the same phylum, bivalves (clams) are a more specialized class and occur mostly on stable, coarse sand or sand-gravel mixtures, at depths < 4-10 m. Bivalves are generally absent on silty substrates.

Water temperature, pH, current velocity and substrate can influence the type and numbers of benthic species in a lentic system (Covich et al. 1999). Increased quantity of organic matter can also increase invertebrate density, because dead organic matter is one of the main sources of energy for benthic invertebrates in shallow water. Water depth also plays an important role in benthic productivity. In an Ontario lake, 68% of invertebrate biomass was found in depths < 2.5 m due to higher nutrient availability, in turn caused by more water movement, habitat diversity, light, oxygen and carbon dioxide that occur in shallow waters (Keast and Harker 1977). When shoreline reaches have gentler slopes, a greater amount of the littoral zone experiences these surface water movements, as well as exposure to light, oxygen and carbon dioxide. The presence of macrophytes, themselves limited by each of the physical lake characteristics described here, aids in littoral-zone productivity by providing organic matter as food from decaying and live tissues, as well as refuge from predators for several macroinvertebrates (Randall et al. 1996).

Exposure and fetch may also be important factors in determining productivity of a littoral zone. Exposure can increase turbidity and influence benthic sediments (Randall et al. 1996). Shorelines exposed to high wind and waves may be suboptimal for macrophytes due to the mechanical damage moving water can inflict. In areas that are protected from waves, macrophytes may develop a layer of sediment on the photosynthetic surface of the leaves due to a lack of water movement, consequently reducing photosynthetic potential. On the other hand, species richness of macrophytes may peak at intermediate levels of exposure, because there may be both positive and negative aspects of wave action on plants (Randall et al. 1996). Longer fetch distances directly increase wave height, and in deep lakes, such as Rainy Lake, wavelength is symmetrical until waves enter the shallow littoral zones, during which time they simutaniously increase in height, and slow down causing them to become asymmetrical and unstable (Witzel 2001). In littoral zones, severe wave action extends to the lake bottom and can prevent sedimentation and the establishment or growth of macrophytes. This thesis is an attempt to generalize the effects of water temperature and movement, pH, the presence of macrophytes, substrate type and water depth into coarse-scale physical lake characteristics.

Bottom substrate, used in previous studies to estimate the value of adult lake sturgeon habitat (Threader et al. 1998), plays a large role in supporting benthic prey. Seyler (1997) noted the absence of lake sturgeon feeding over bedrock and clay, attributing this behavior to the lack of prey on these substrates. Lake sturgeon were found in autumn at higher densities on substrates of sand and organic matter, corresponding to apparent selection for prey, and at successively lower densities on cobble and gravel. In the HSM that Haxton et al. (2008) validated, silt had the highest value as a substrate supporting lake sturgeon prey, followed by sand, gravel and cobble. Using telemetry data in Rainy Lake, Adams et al. (2006b) found that adult lake sturgeon selected areas with shallow rock reefs or shoreline reaches with depths < 15 m during July and August. Halliday (2010) extended the correlation between location frequency in the Adams et al. (2006b) study to higher use of reaches of Rainy Lake shoreline dominated by soft (silt and sand) substrates.

Earlier documentation suggests that adult lake sturgeon routinely occupy depths < 9 m (Peterson et al. 2007), but recent work suggests they may actually prefer depths < 6.5 m (Haxton et al. 2008). In the Groundhog River, Ontario, lake sturgeon preferred depths

< 6 m in autumn, during a time when they are likely heavily feeding to prepare for winter months (Seyler 1996).

Study area

Rainy Lake and the Namakan Reservoir, which includes Kabetogama and Namakan lakes, are situated on the U.S./Canadian border east of International Falls, Minnesota, and Fort Frances, Ontario. Voyageurs National Park encompasses portions of Rainy Lake's south arm and has a total area of 88,628 ha, 34,400 ha of which is water. This study will be restricted to the South Arm of Rainy Lake, the largest surface area at 49,200 ha (Adams et al. 2006a; Fig. 1).

Two smaller lakes, Kabetogama and Namakan, are situated south and south east of Rainy Lake respectively. Hydroelectric dams were constructed at Fort Frances during the early 1900s, which caused average water levels to rise and annual water fluctuations to increase (Kallemeyn et al. 2003). Water levels in Rainy Lake have been subject to two different management regimes since 1970, presenting a natural experiment to investigate how the water level management can influence macroinvertebrate community structure (McEwen and Butler 2008). The management regime in 1970 allowed a 2.5 m lake-level drawdown throughout the winter while the 2000 regime only allowed a drawdown of 1.5 m. Bivalve and snail abundance increased under the new regime in eulittoral communities with decreased ubiquity of bivalves in the sublittoral community. Decreases in the abundance of two mayfly genera (*Caenis* and *Hexagenia*) and a family of caddisflies (Polycentropodidae) occurred after the implementation of the 2000 regime, though *Hexagenia* only decreased slightly.

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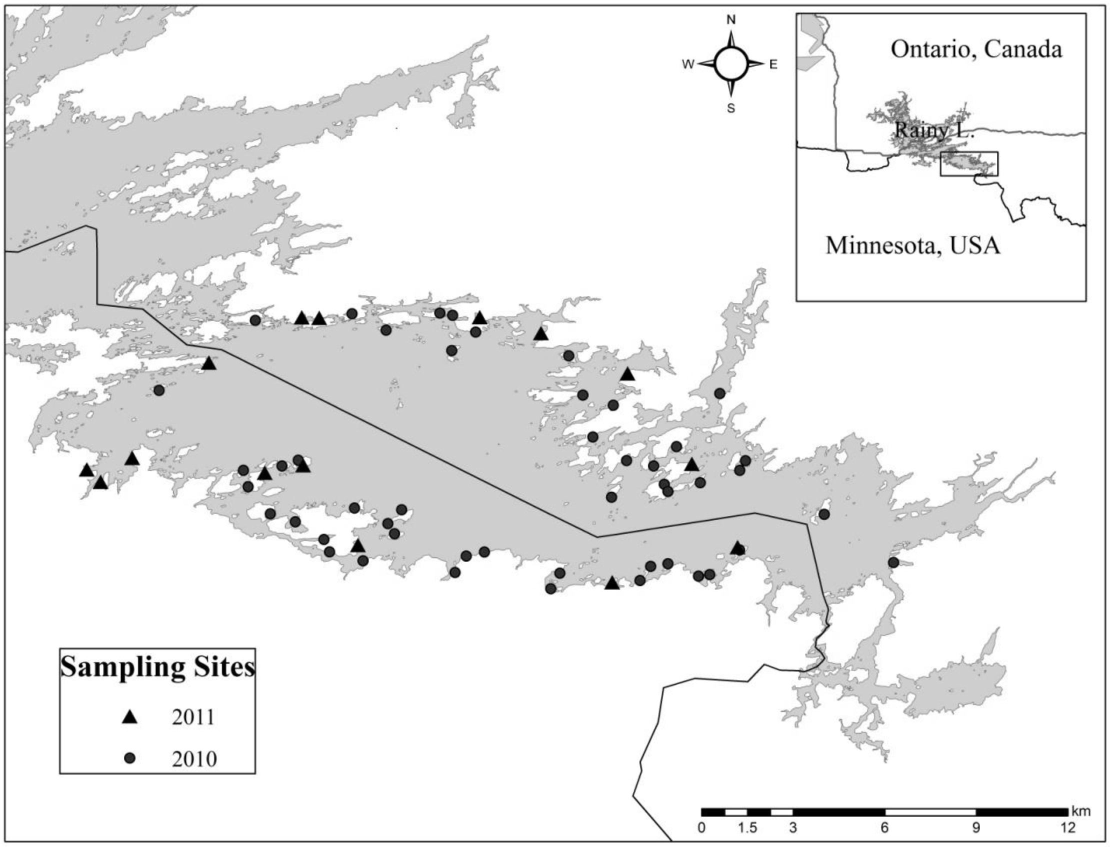

Figure 1. Map of the Rainy Lake study area and the sample site locations for the summer of 2010 (*n* = 48) and 2011 (*n* = 15).

<u>Sampling protocols to survey potential lentic feeding areas</u>

This project required sampling in areas with a wide range of substrate types, littoral-zone slopes, and macrophyte abundances, making the selection of the appropriate sampling technique difficult (Downing and Rigler 1984). The Ekman grab, the most common sampling technique for benthic material, is not capable of collecting reliable samples from substrates harder than sand (Rosenberg et al. 2001). The Peterson grab will pick up more resistant material than the Ekman, but it still will not sample well from bedrock. A third type of sampler is the substrate corer, which uses its own weight to penetrate sediment with a long, open core tube. Substrate corers also do not work in substrates that provide resistance to penetration. Developed for rocky shorelines, the rock pick technique entails collecting individual rocks and picking invertebrates from them, but is not suitable for shorelines that are not rocky (Rosenberg et al. 2001). Activity traps are modified minnow traps that collect larger invertebrates like crayfish, leeches and dragonflies, but they are not suited for smaller invertebrates. The kick-and-sweep method is highly versatile and can be used on all substrates (Rosenberg et al. 2001). The shoreline is sampled by kicking up the substrate and then sweeping above the disturbed area with a D-net to collect dislodged or escaping invertebrates. During this time the net is kept in continuous forward motion or lifted out of the water to prevent the loss of specimens.

The Ontario Benthos Biomonitoring Network (OBBN) describes a near-shore lake sampling method that uses a kick-and-sweep methodology (Jones et al. 2004; Fig. 2). Lake segments become the sampling units in an inventory suited to shallow, wadeable, near-shore areas. At each lake segment, a total of 100 invertebrates are collected and a minimum of one transect to a depth of 1 m must be completed during the collection of the sample. If invertebrates are abundant at a lake segment, time spent sampling and distance covered can be reduced. Sampling time can be reduced because sampling effort is recorded as area covered and time spent collecting. The sampling effort allows unbiased comparisons between lake segments.

Sampling design

Choice of variables defining shoreline characteristics was influenced by the ability to find practical sites for sampling; therefore, a suitable sampling design was developed during preliminary investigation of the study sites (Table 1). The sampling design included eight

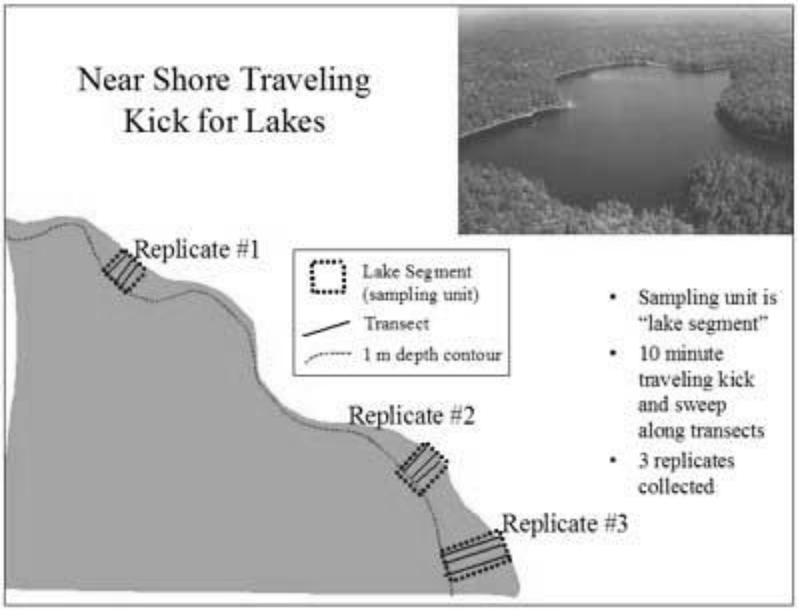

Figure 2. Traveling kick-and-sweep sampling method developed for biomonitoring of lakes (Jones et al. 2004).

categories of shoreline (Table 2). Littoral-zone slope was estimated by calculating the angle from the shoreline to a distance where water depth reached 3 m. A total of three transects were measured and averaged for an accurate measure of slope. Fetch and wind and wave exposure were estimated from topographic maps as the longest unobstructed distance across water in the prevailing wind directions and the angle of exposure to wind and waves respectively. Intermediate values were not investigated, so that extremes in shoreline characteristics could be compared in a series of multivariate models, i.e., variable definitions did not account for areas of fetch from 1-2 km, littoral-zone slopes from 8.5-11.3˚, and exposure angles from 70-100˚ spanning open water to a distance of 100 m at short fetches and 2 km at long fetches. In August 2011, benthic macroinvertebrate communities were sampled at 15 random shoreline locations. Inferences drawn from the 2010 sampling and resulting multivariate modeling were used to guide further investigation of models for fetch, exposure and littoral-zone slope as they affected benthic macroinvertebrate distribution from these random samples.

Table 1. Descriptions of binary variable levels for fetch, slope and exposure that influenced site selection in 2010.

	Description
Long fetch	An unobstructed distance > 2 km across water
Short fetch	An unobstructed distance < 1 km across water
Gentle littoral-zone slope	Littoral zones with a slope < 8.53˚ to 3 m depth
Steep littoral-zone slope	Littoral zones with a slope > 11.31˚ to 3 m depth
Exposed	Shoreline locations with > 100˚ of exposure
Protected	Shoreline locations with < 70˚ of exposure

Table 2. Shoreline category descriptions for the sampling design used to characterize benthic sediments and macroinvertebrate communities in Rainy Lake, Minnesota and Ontario. Sampling in 2010 was steered to four sites matching each description.

	Shoreline descriptions		
Acronym	Littoral-zone slope	Fetch	Wind and wave exposure
SSP	Steep	Short	Protected
SLP	Steep	Long	Protected
GSP	Gentle	Short	Protected
GLP	Gentle	Long	Protected
SSE	Steep	Short	Exposed
SLE	Steep	Long	Exposed
GSE	Gentle	Short	Exposed
GLE	Gentle	Long	Exposed

Field methods

Data collection occurred over a 10-day period in each of June, July and August 2010. The sampling procedure followed a modified version of OBBN’s near-shore lake sampling method. Modifications included sampling as deep as possible within equipment constraints to extend transects as far as possible to a range of lake sturgeon feeding habitats. A second modification was to sample non-adjacent shoreline reaches. During

June, two shoreline reaches were sampled for each of the eight shoreline categories. (Table 2). One set of these reaches was sampled again during July and August to track macroinvertebrate community and biomass changes from month to month. Along with the repeated sampling, there were two more replicates of each variable combination completed for both July and August. Therefore, throughout the three months of fieldwork in 2010 there were six replicates sampled for each variable combination, as well as repeated sampling of eight replicates in July and August. Substrate type was recorded at each sampling location, classified as fine (organic-sand), medium (gravel-cobble) and coarse (boulder-bedrock). The aquatic macrophyte community was classified into two vegetation types, either rooted or emergent, and then into five cover categories: 0%, 1-25%, 26-50%, 51-75% or 76-100%.

Benthic macroinvertebrates were collected in a D-net along 50-cm wide transects at a rate of 2 m travelled per min from the shoreline until a minimum of 100 individuals were collected. Individuals captured in the D-net were removed, sorted by taxonomic group (Table 3), and preserved in glass vials filled with 70% alcohol solution. At a central processing location, the content of each vial was weighed, and counted. Biomass per square metre (hereafter, biomass, in units of mg/m^2) was estimated for each taxon from the distance travelled along up to seven complete transects and their corresponding area.

Statistical analysis

To summarize how macroinvertebrate community structure varied among sample sites and to evaluate how this variation was related to coarse-scale physical lake characteristics, macrophytes and substrates, I used a nonmetric multidimensional scaling

Table 3. List of invertebrate taxa collected during the study. Asterisks indicate invertebrates included in the subset of log transformed biomass data used during model testing.

Common Name	Level of Identification	Scientific Name
Beetles	Order	Coleoptera
Bivalves*	Class	Bivalvia
Bloodworms	Genus	*Glycera*
Caddisflies*	Order	Trichoptera
Crayfish*	Order	Decapoda
Damselflies	Suborder	Zygoptera
Dragonflies*	Suborder	Anisoptera
Leeches*	Subclass	Hirudinea
Mayflies*	Order	Ephemeroptera
Midges	Family	Chironomidae
Mosquitoes	Family	Culicidae
Scuds	Order	Amphipoda
Snails*	Class	Gastropoda
Sowbugs	Order	Isopoda

(NMS) ordination of macroinvertebrate biomass data in PC-ORD (McCune and Grace 2002). The macroinvertebrate biomass data from 2010 comprised the main matrix and underwent a z-transformation to standardize values across the three months. Also, a standard value of 0.9488 (the minimum value) was added across all months to the z-transformed data to eliminate negative values. A secondary matrix of environmental variables held all of the categorical data (slope, fetch, exposure, substrate type, and vegetation type), which were used to illustrate groups in the ordination and quantitative data (fetch, angle of exposure and average slope; Table 2), were used to illustrate correlations with invertebrate communities as vectors in the NMS. Unlike later portions of the statistical analysis and model building, all invertebrate taxa (Table 3) were included in the main matrix.

To help define the habitat preferences of benthic macroinvertebrate communities and to track monthly biomass trends, coarse-scale lake characteristics were examined using the practical information-theoretic approach to general linear modeling. This approach required a subset of log-transformed invertebrate biomass data considered to be important in the sturgeon diet (Table 3). A set of candidate multivariate analysis of variance (MANOVA) models linking this subset of the biomass data to slope, fetch, exposure and any two-way variable interactions, including the month of sampling, were evaluated for parsimony and fit. Only two-way interactions were considered due to a limited number of replicates when differences in the macroinvertebrate community structure were considered by month. For model evaluation, the residual sum of squares cross-products matrix (SSCP) was calculated in the Statistical Package for the Social Sciences (SPSS 2007), and an adjusted Akaike's Information Criterion (AIC) for small samples (AIC_c) was derived for each MANOVA (Burnam and Anderson 2002). AIC_c, AIC_c differences (Δ_i), and the corresponding Akaike weights (w_i) indicated the best model. Finally, univariate regressions were used to compare the relationship among inverterbrate biomass estimates in August 2011 and variables that were significant in the best model from the 2010 data.

In a study by Adams et al. (2006b), 41 lake sturgeon ($\geq$ 8 kg, with a mean fork length of 1.2 m) were implanted with radio transmitters and then relocated aerially once per week and by boat two to three times per week during the summer seasons of 2003 and 2004 in Rainy Lake. Any areas with frequent locations were re-sampled by boat during May and June due to the difficulty in recognizing individual signals from air. Locations corresponding to individuals not in the study area, locations collected outside the period of interest, and locations distant from the littoral zone (> 200 m from shoreline) were excluded. Out of 413 locations of lake sturgeon, 141 were used for examination of feeding habitat use during July (*n* = 46) and August (*n* = 31) in 2003, and June (*n* = 7), July (*n* = 27) and August (*n* = 30) in 2004. Shoreline characteristics corresponding to these locations were classified into similar categories as other shoreline reaches in this study: either protected (< 85˚ of exposure) or exposed (> 85˚ of exposure), with short (< 1500 m) or long (> 1500 m) fetches, and with gentle or steep littoral zones (based on lake map bathometric contours). Month and year of location were tested along with these classes using Poisson loglinear modeling to describe the lake sturgeon locations according to the same factors in the best-fit model for macroinvertebrate biomass.

RESULTS

Macroinvertebrate community structure

The first and second axes represented the most variance in macroinvertebrate biomasses with a coefficient of determination summing to 0.756. Axes 1 through 3 had coefficient of determination values of 0.572, 0.185 and 0.156, respectively. Axis 1 seems to explain most macroinvertebrate abundance while axis 2 shows some community separation (Figures 3-5). The angles and lengths of radiating lines in Figures 3 through 5 indicate the direction and strength of relationships of the variables with the ordination scores. As the lines radiate out from the centroid, representation of fetch distances becomes longer, angle of exposure becomes larger, and littoral-zone slope becomes gentler. For the ordination a coefficient of determination cut-off value of 0.01 was used.

Two clear community assemblages are apparent in the ordinations, one comprising leeches, true bugs, and bivalves, the other dragonflies, midges, caddisflies and sowbugs. The two are in the same position along the slope-fetch gradient and are separated in the plane of the exposure vector, suggesting that the second assemblage is associated with smaller angles of exposure. Snails occupy shoreline reaches with long fetch and steep littoral-zone slopes. Exposure is not as strongly correlated with the difference in the invertebrate communities.

The substrate classes of different shoreline reaches appear to separate along the fetch-slope gradient (Fig. 3). Coarse substrates are more common along shoreline reaches with long fetch and steep littoral-zone slopes, while finer sediments are more common at short fetches and on gentle littoral-zone slopes. Biomass of snails, beetles and crayfish was higher at sites with medium and coarse substrates, while sowbugs, caddisflies, midges, and dragonflies were more abundant at sites with finer substrates. When plotted with emergent or rooted vegetation (Figs. 4 and 5), sites with long fetch and gentle littoral-zone slopes are shown to have less vegetation cover.

Changes in macroinvertebrate biomass June through August

Shoreline reaches with gentle littoral-zone slopes and short fetch supported the greatest biomass for mayflies in June (Fig. 6). In the eight sites revisited throughout the summer, and for averaged biomass among 75% of the shoreline categories, mayflies experienced a reduction in biomass by July. Throughout the summer snail biomass increased in abundance from June onward except at GSP reaches (Fig. 7). Shoreline categories of GSE and GSP appeared to yield greater biomass of dragonflies (Fig. 8).

The contribution to total biomass by different macroinvertebrates fluctuated throughout three month sampling period of 2010 (Fig. 9). In June contributions to total biomass from leeches, scuds, crayfish, mayflies and dragonflies were most important. Crayfish only contributed to an eighth of the biomass during this month. July and August had almost three quarters of their biomass originating from the presence of crayfish and snails at sampling sites.

Modeling effects of physical characteristics and season on the macroinvertebrate community

Modeling biomass of macroinvertebrates important in the lake sturgeon diet considered ten competing models, including the complete model consisting of all possible parameters and two-way interactions, and one model (Model 6) consisting of only the three main-effect variables used to classify shoreline reaches (Table 4). When ranked from least to most informative, Model 10 is by far the most informative, followed by Model 6 (Table 5). Fetch and the interactions between fetch and exposure and between season and littoral-zone slope best described biomass. Model fit was not equal across all of the dependent variables, where significant effects of physical lake characteristics occur for biomass of caddisflies (R^2 = 0.309), snails (R^2 = 0.228), bivalves (R^2 = 0.248), crayfish (R^2 = 0.163), dragonflies (R^2 = 0.148), and total biomass (R^2 = 0.239), while there is little to no predictive power for biomass of mayflies (R^2 = 0.052) and leeches (R^2 = -0.085; Table 6). Shoreline reaches with short fetch have higher biomass of bivalves. The interaction between fetch and exposure helps in predicting biomass of caddisflies, dragonflies and snails. Both caddisflies and dragonflies are found with a large angle of

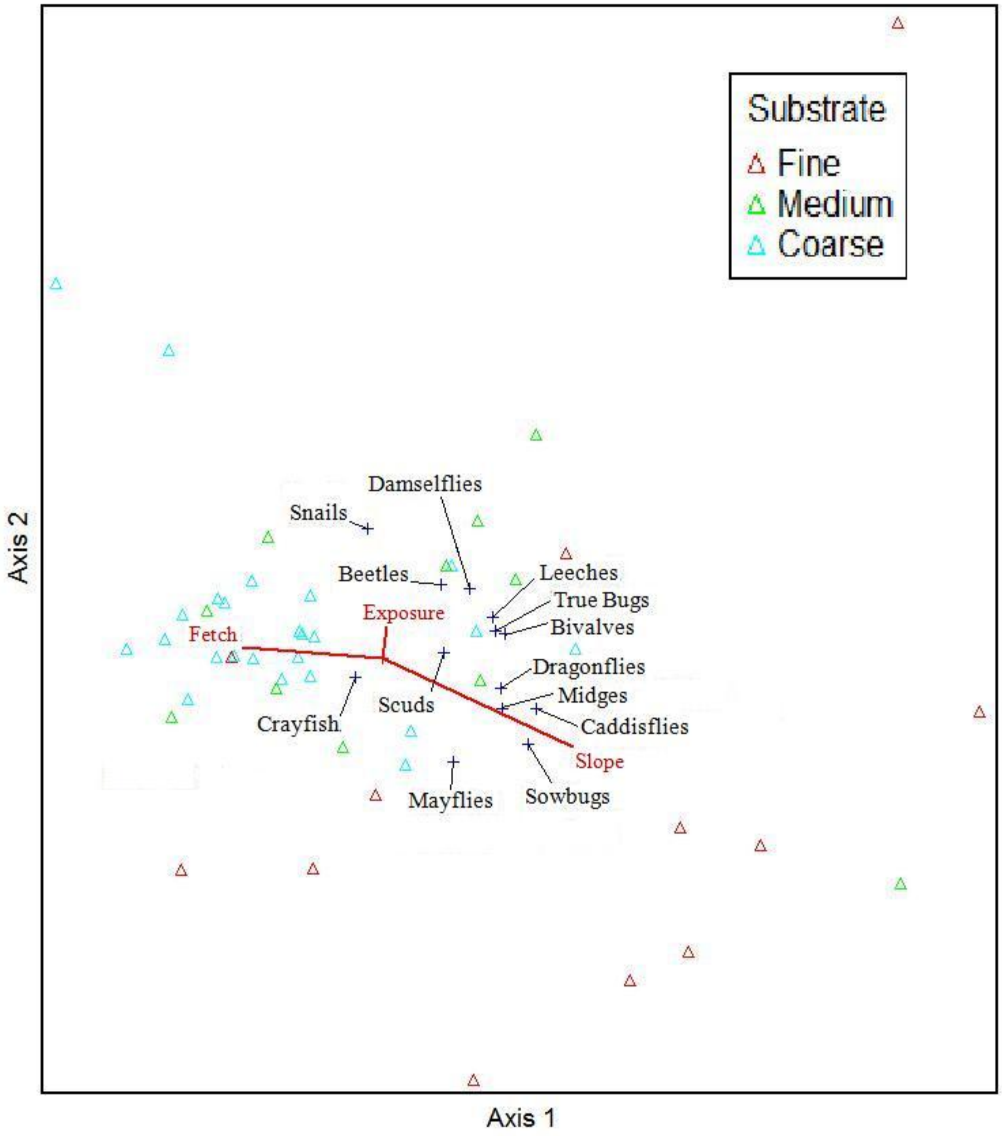

Figure 3. Joint plot depicting the solution of a nonmetric multidimensional scaling (NMS) ordination using substrate as a grouping variable. Fine substrates include sand and smaller material, medium substrates include gravel and cobble, and coarse substrates include boulder and bedrock. As vectors radiate out from the centroid slopes become gentler, fetches become longer and angles of exposure become wider.

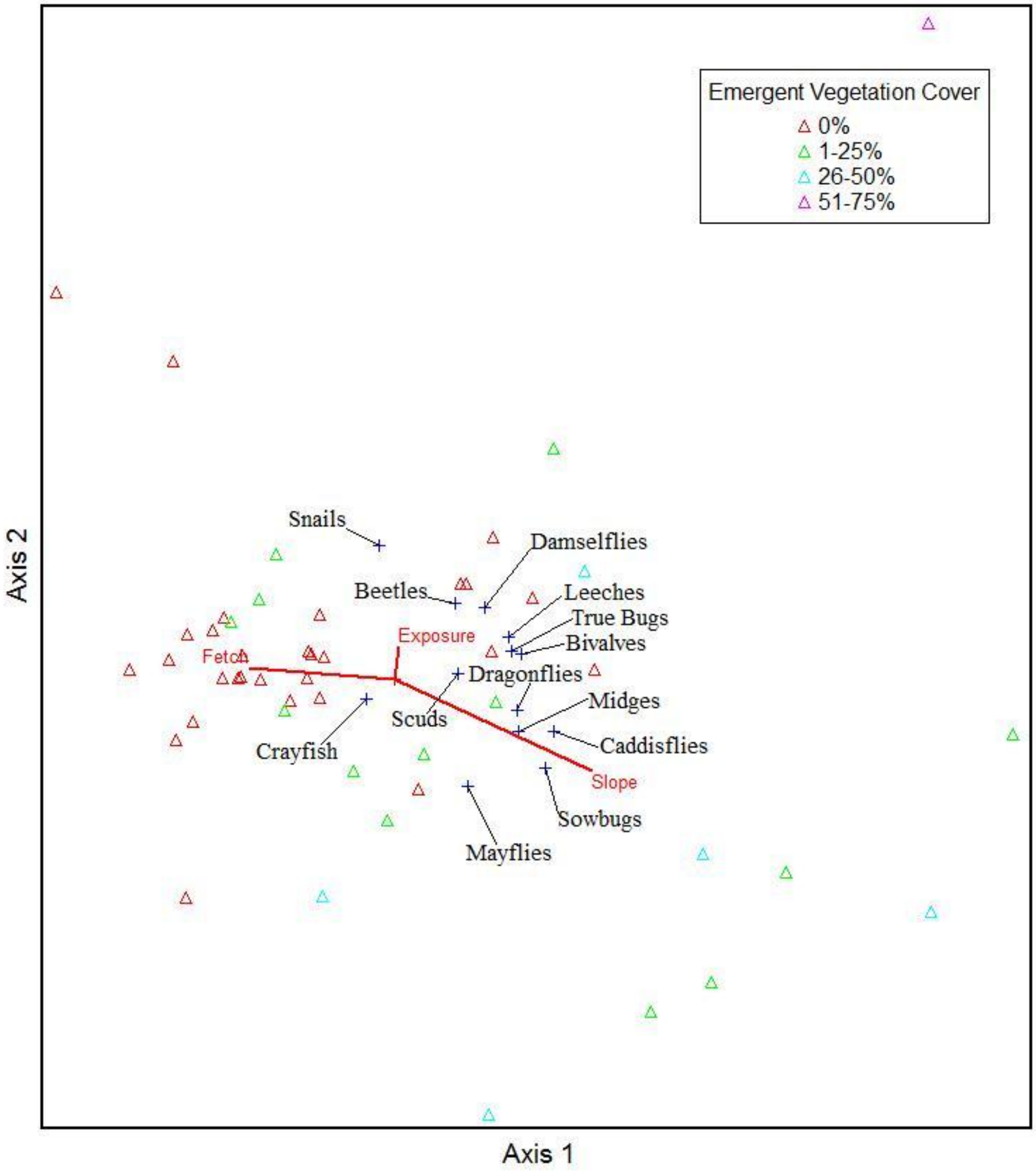

Figure 4. Joint plot depicting the solution of a NMS ordination using emergent vegetation cover as a grouping variable. As vectors radiate out from the centroid slopes become gentler, fetches become longer and angles of exposure become wider.

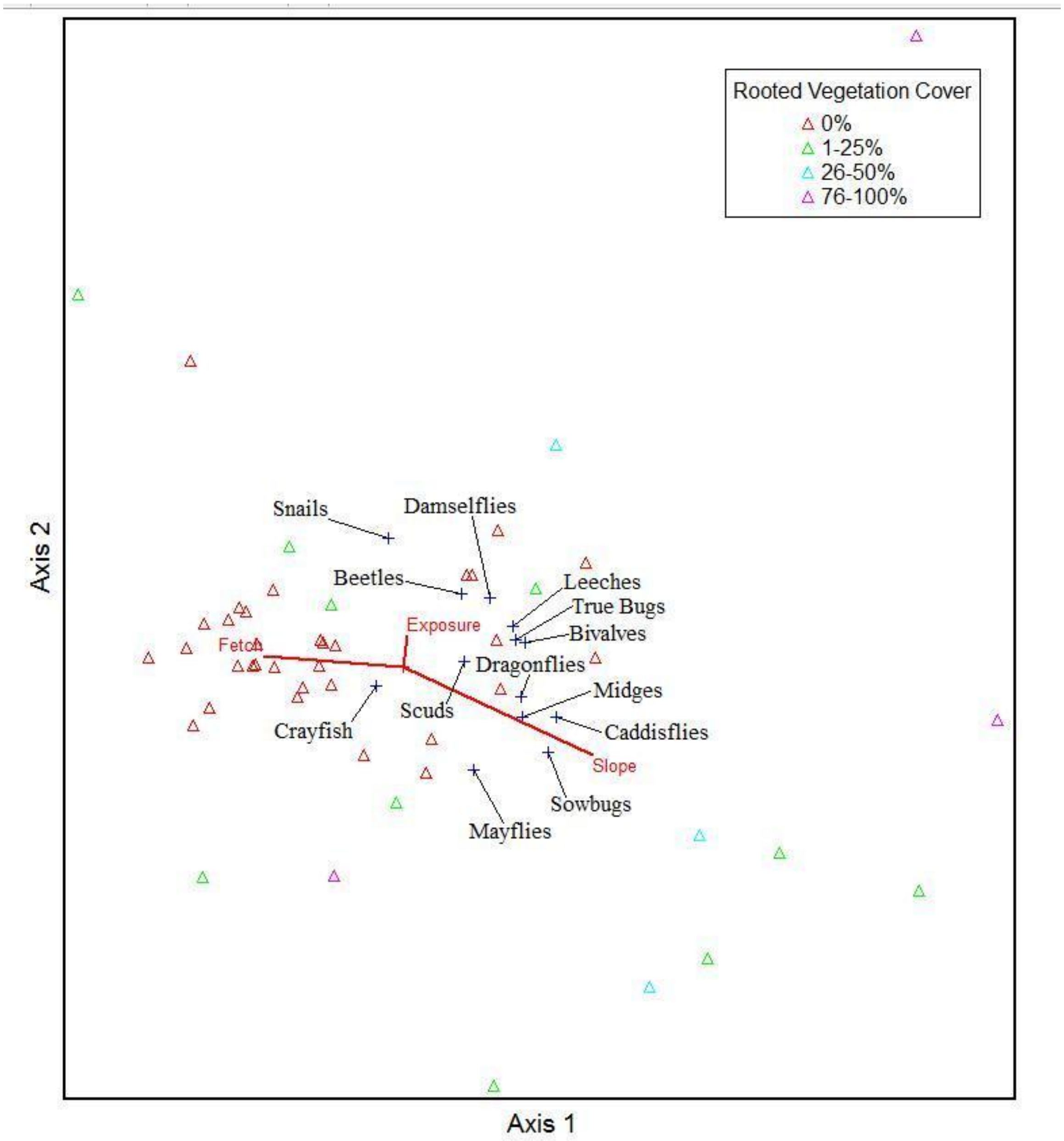

Figure 5. Joint plot depicting the solution of a NMS ordination using substrate type as a grouping variable. As vectors radiate out from the centroid slopes become gentler, fetches become longer and angles of exposure become wider.

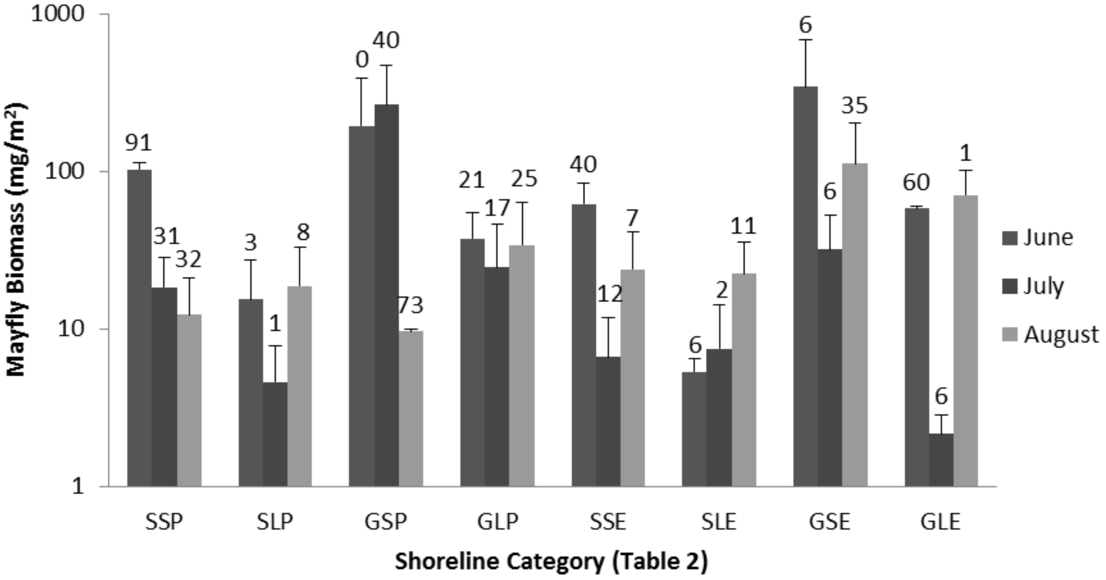

Figure 6. Average mayfly biomass (mg/m^2) by shoreline type and month of collection. Numbers displayed above each column represent biomass collected through the repeated sampling of eight sites from June through August, 2010. Error bars represent standard error.

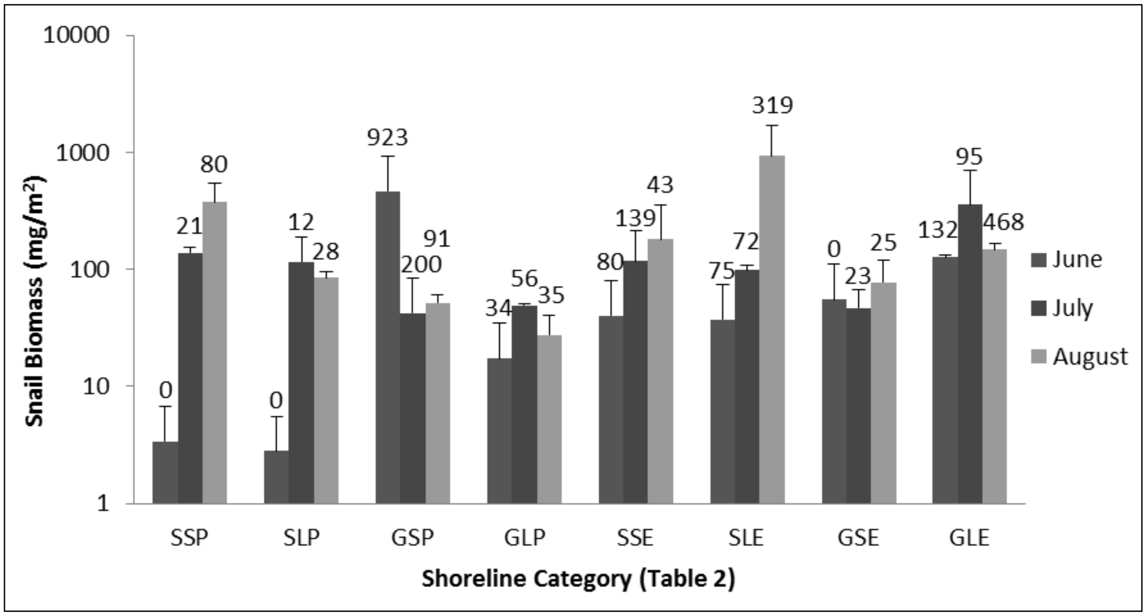

Figure 7. Average snail biomass (mg/m^2) by shoreline type and month of collection. Numbers displayed above each column represent biomass collected through the repeated sampling of eight sites from June through August, 2010. Error bars represent standard error.

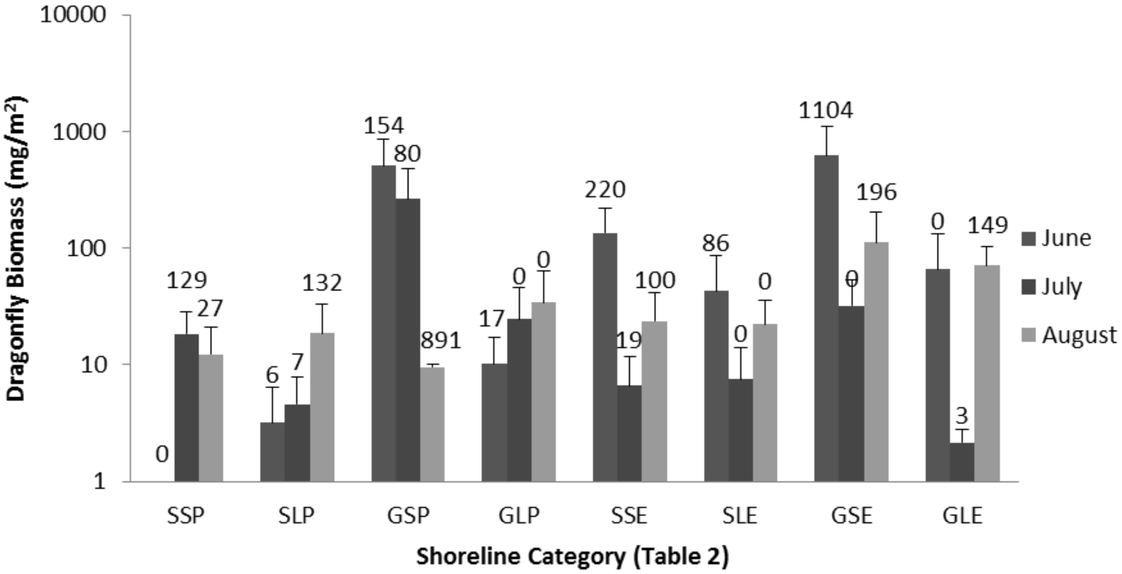

Figure 8. Average dragonfly biomass (mg/m^2) by shoreline type and month of collection. Numbers displayed above each column represent biomass collected through the repeated sampling of eight sites from June through August, 2010. Error bars represent standard error.

shoreline exposure and short fetch, while snails are more often found at exposed sites with long fetch. Bivalves, crayfish, snails and total biomass can be explained in part by the interaction between season and slope. In June and July, bivalves are more prevalent on gentle littoral-zone slopes, and biomass of snails and crayfish and total biomass are higher on steep littoral-zone slopes.

There were negative relationships between total macroinvertebrate biomass, fetch, angle of shoreline exposure and steeper littoral-zone slopes (Tables 7, 8 and 9). As predicted by the best model fitting the 2010 data (Table 6), biomass estimates from sampling in August 2011 confirm that longer fetch corresponds to a lower biomass of bivalves (Fig. 10). Similarly, an inverse linear relationship occurs between fetch and

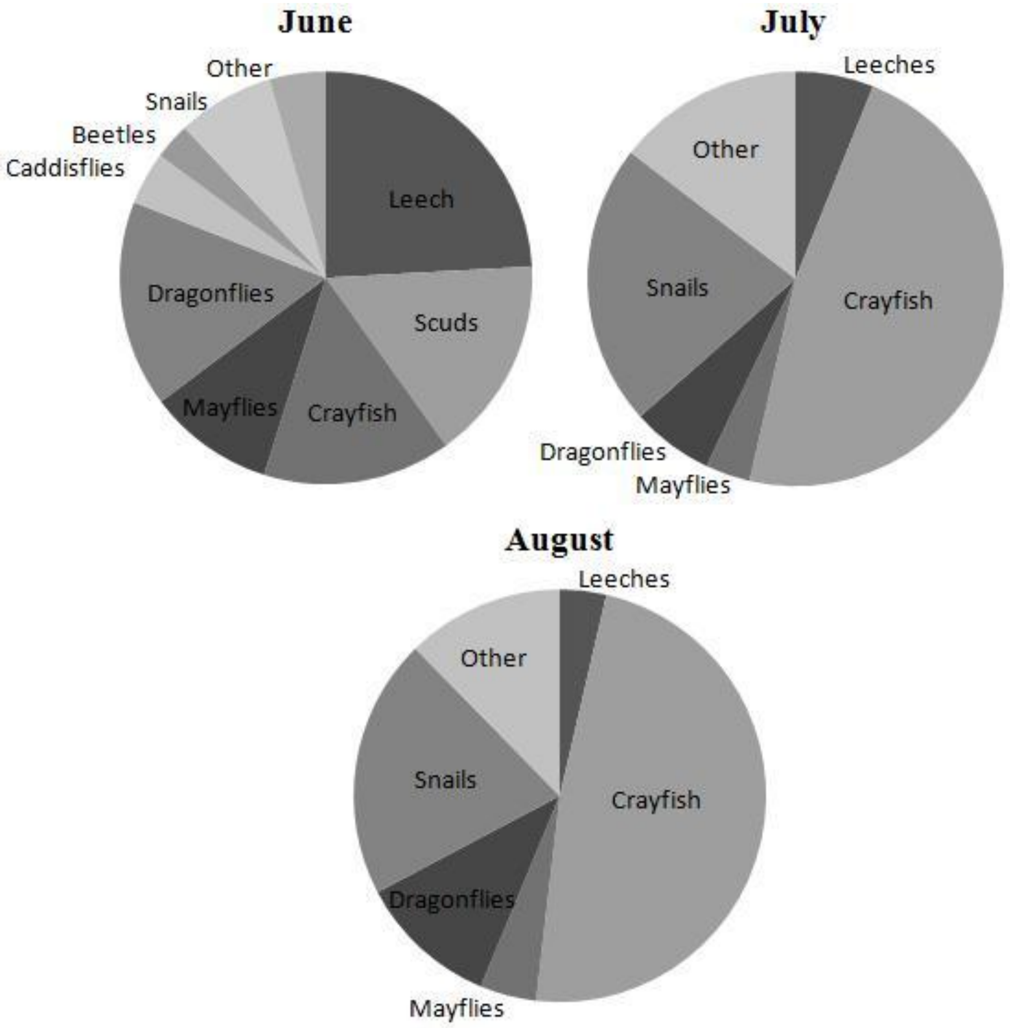

Figure 9. Macroinvertebrate contributions to total biomass in June, July and August, 2010.

biomass of mayflies and caddisflies (Fig. 10). Caddisfly biomass was lower at higher angles of shoreline exposure (Fig. 11). Shoreline reaches with shorter fetch and larger angles of exposure had more caddisfly biomass than reaches with small angles of exposure as indicated from Model 10. Bivalve biomass is lower at larger angles of shoreline exposure.

Table 4. Candidate models and their corresponding parameters used to explain the community of macroinvertebrates found on Rainy Lake shorelines. Intercepts were included in all model fitting.

Model	Model parameters
1	Fetch, slope, exposure, season, fetch × slope, fetch × exposure, slope × exposure, season × fetch, season × slope, season × exposure
2	Fetch, slope, season, fetch × slope, fetch × exposure, season × fetch, season × slope, season × exposure
3	Fetch, fetch × exposure, season × fetch, season × slope, season × exposure
4	Fetch, slope, season, fetch × slope, fetch × exposure, season × exposure
5	Fetch, season, fetch × exposure, season × exposure
6	Fetch, slope, exposure
7	Fetch, slope, exposure, season
8	Fetch, season, fetch × exposure
9	Fetch, slope, season, fetch × exposure
10	Fetch, fetch × exposure, season × slope

Table 5. Models of the Rainy Lake macroinvertebrate community from Table 4 ordered from most to least informative. Lower AIC_c indicates better model representation of biomass of dominant taxa in the lake sturgeon diet (Table 3). ΔAIC_c represents the relative change in AIC_c between each model and the best fit model and w_i is the Akaike weight showing the weight of evidence for best model.

Model	Number of parameters	AIC_c	ΔAIC_c	w_i
10	5	914.94	0.00	0.99996
6	4	935.54	20.61	0.00003
8	5	941.65	26.72	0.00000
3	9	945.37	30.44	0.00000
9	6	946.08	31.14	0.00000
7	6	953.32	38.38	0.00000
5	7	955.08	40.14	0.00000
4	9	978.16	63.23	0.00000
2	13	1010.46	95.52	0.00000
1	15	1039.72	124.79	0.00000

Table 6. Significance of factors in three models describing macroinvertebrate habitat selection based field sampling in 2010. Fetch (0) = short fetch, fetch (1) = long fetch, exposure (0) = exposed, slope (0) = gentle, slope (1) = steep, August (0) = June and July, August (1) = August and June (0) = July and August. Leeches and mayflies are not included due to a lack of significance. Parameters are indicated in boldface where $p < 0.05$.

Taxon	Factors	β	S.E.	Odds ratio	Odds ratio Lower	Odds ratio Upper	*p*
Caddisflies	Fetch (0)	0.58	0.64	1.78	0.93	3.38	0.38
	Fetch (0) × exposure (0)	1.79	0.64	5.99	3.15	11.39	**0.01**
	Fetch (1) × exposure (0)	-0.23	0.64	0.80	0.42	1.51	0.72
	August (0) × slope (0)	0.14	1.11	1.16	0.38	3.52	0.90
	August (0) × slope (1)	-1.15	0.79	0.32	0.14	0.70	0.15
	August (1) × slope (0)	1.74	1.36	5.71	1.46	22.34	0.21
	June (0) × slope (0)	-1.52	0.79	0.22	0.10	0.48	0.06
	June (0) × slope (1)	-0.02	0.79	0.98	0.45	2.15	0.98
Bivalves	**Fetch (0)**	0.91	0.40	2.49	1.67	3.71	**0.03**
	Fetch (0) × exposure (0)	-0.48	0.40	0.62	0.42	0.93	0.24
	Fetch (1) × exposure (0)	-0.27	0.40	0.77	0.51	1.14	0.51
	August (0) × slope (0)	-0.02	0.69	0.98	0.49	1.96	0.98
	August (0) × slope (1)	-0.46	0.49	0.63	0.39	1.03	0.36
	August (1) × slope (0)	-1.30	0.85	0.27	0.12	0.64	0.13
	June (0) × slope (0)	1.10	0.49	3.01	1.85	4.92	**0.03**
	June (0) × slope (1)	0.00	0.49	1.00	0.62	1.64	0.99
Crayfish	Fetch (0)	-0.92	1.12	0.40	0.13	1.22	0.42
	Fetch (0) × exposure (0)	-0.32	1.12	0.73	0.24	2.22	0.78
	Fetch (1) × exposure (0)	-1.21	1.12	0.30	0.10	0.91	0.29
	August (0) × slope (0)	1.61	1.93	4.99	0.72	34.56	0.41
	August (0) × slope (1)	-1.76	1.37	0.17	0.04	0.68	0.21
	August (1) × slope (0)	3.43	2.37	30.90	2.89	330.34	0.16
	June (0) × slope (0)	-1.50	1.37	0.22	0.06	0.87	0.28
	June (0) × slope (1)	3.19	1.37	24.17	6.15	94.93	**0.03**
Dragonflies	Fetch (0)	-0.37	0.91	0.69	0.28	1.72	0.69
	Fetch (0) × exposure (0)	2.01	0.91	7.49	3.02	18.58	**0.03**
	Fetch (1) × exposure (0)	-1.35	0.91	0.26	0.11	0.65	0.15
	August (0) × slope (0)	1.68	1.57	5.39	1.12	25.99	0.29
	August (0) × slope (1)	-0.45	1.11	0.64	0.21	1.93	0.69
	August (1) × slope (0)	1.42	1.93	4.15	0.60	28.47	0.46
	June (0) × slope (0)	-1.27	1.11	0.28	0.09	0.86	0.26
	June (0) × slope (1)	0.07	1.11	1.07	0.35	3.27	0.95

Table 6, continued.

Taxon	Factors	β	S.E.	Odds ratio	Odds ratio Lower	Odds ratio Upper	*p*
Snails	Fetch (0)	0.42	0.69	1.52	0.76	3.02	0.55
	Fetch (0) × exposure (0)	-0.07	0.69	0.93	0.47	1.85	0.92
	Fetch (1) × exposure (0)	1.44	0.69	4.23	2.12	8.41	**0.04**
	August (0) × slope (0)	0.89	1.19	2.45	0.74	8.06	0.46
	August (0) × slope (1)	-0.61	0.84	0.54	0.23	1.26	0.47
	August (1) × slope (0)	1.36	1.46	3.88	0.90	16.70	0.36
	June (0) × slope (0)	0.53	0.84	1.71	0.73	3.96	0.53
	June (0) × slope (1)	2.97	0.84	19.46	8.37	45.21	**0.00**
Total Biomass	Fetch (0)	0.85	0.49	2.35	1.43	3.85	0.09
	Fetch (0) × exposure (0)	0.04	0.49	1.04	0.63	1.70	0.94
	Fetch (1) × exposure (0)	0.14	0.49	1.15	0.70	1.89	0.77
	August (0) × slope (0)	1.28	0.86	3.60	1.53	8.47	0.14
	August (0) × slope (1)	-0.85	0.60	0.43	0.23	0.78	0.17
	August (1) × slope (0)	1.55	1.05	4.70	1.65	13.39	0.15
	June (0) × slope (0)	-0.74	0.60	0.48	0.26	0.87	0.23
	June (0) × slope (1)	1.35	0.60	3.87	2.12	7.09	**0.03**

Table 7. Significant invertebrate trends as they relate to changes in fetch using verification data collected in 2011. The natural log of fetch was used in linear regression models (Fig. 10). Effects of fetch are indicated in boldface where $p < 0.05$.

	R^2	β	Standard error	F	*t*	*p*
Bivalves	0.29	-10.66	4.62	5.32	-2.31	**0.04**
Caddisflies	0.29	-22.00	9.61	5.24	-2.29	**0.04**
Crayfish	0.04	-174.35	233.41	0.56	-0.75	0.47
Dragonflies	0.13	-159.67	112.83	2.00	-1.42	0.18
Mayflies	0.26	-22.91	10.77	4.52	-2.13	**0.05**
Snails	0.03	-42.17	65.72	0.41	-0.64	0.53
Total biomass	0.14	-431.76	295.61	2.13	-1.46	0.17

Slope was significantly related to biomass of bivalves, dragonflies and caddisflies (Table 9); all three taxa had greater biomass in August 2011 on gentler littoral-zone slopes (Fig. 12).

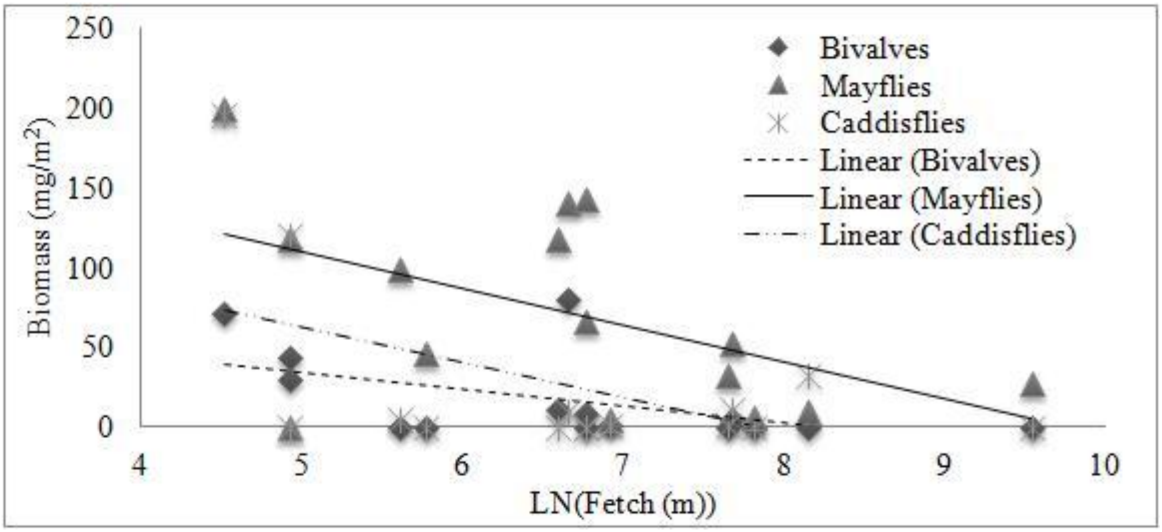

Figure 10. Significant linear relationships of bivalve, mayfly and caddisfly biomass with fetch.

Table 8. Significant invertebrate trends as they relate to changes in angle of exposure using verification data collected in 2011. Statistics correspond to linear regression models (Fig. 11). Effects of angle of exposure are indicated in boldface where *p* < 0.05.

	R^2	β	Standard error	F	*t*	*p*
Bivalves	0.51	-0.33	0.09	13.26	-3.64	**<0.01**
Caddisflies	0.30	-0.52	0.22	5.53	-2.35	**0.04**
Crayfish	0.15	-7.70	5.15	2.24	-1.50	0.16
Dragonflies	0.12	-3.51	2.66	1.74	-1.32	0.21
Mayflies	0.23	-0.51	0.26	3.97	-1.99	0.07
Snails	0.03	1.03	1.53	0.46	0.68	0.51
Total biomass	0.18	-11.54	6.73	2.94	-1.71	0.11

Modeling physical lake characteristics and season on lake sturgeon locations

Comparison of lake sturgeon locations in 2003 with the factor set in Model 10 indicated significant relationships of fetch, exposure and an interaction between month and slope (Table 10). Lake sturgeon were almost twice as likely in 2003 to occupy

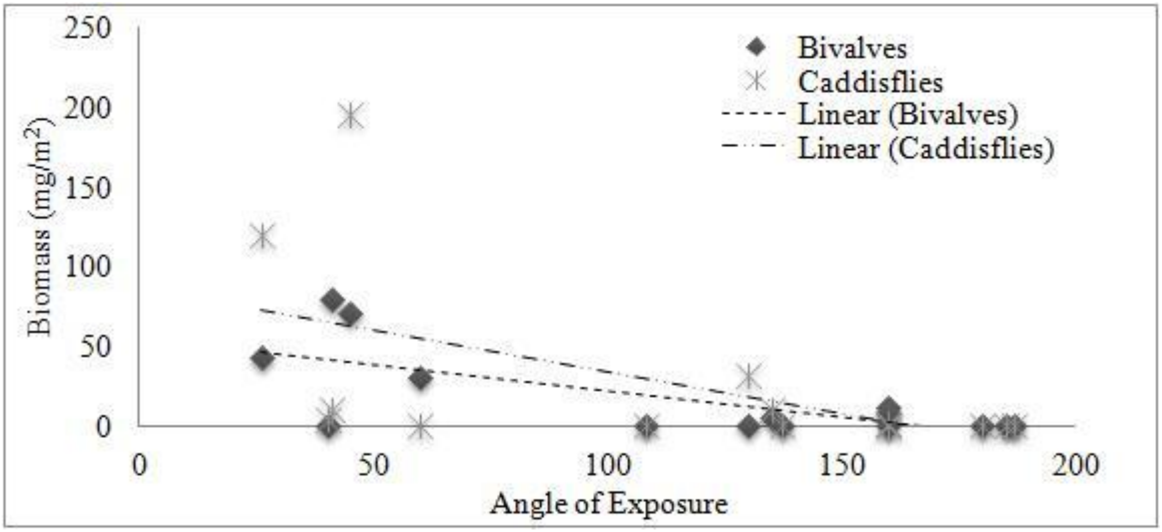

Figure 11. Significant linear relationships of bivalve and caddisfly biomass with angle of exposure.

Table 9. Significant invertebrate trends as they relate to changes in littoral-zone slope using the verification data collected in 2011. Statistics correspond to linear regression models (Fig. 12). Effects of littoral-zone slope are indicated in boldface where *p* < 0.05.

	R^2	β	Standard error	F	*t*	*p*
Bivalves	0.33	0.43	0.17	6.41	2.53	**0.03**
Caddisflies	0.32	0.87	0.36	5.97	2.44	**0.03**
Crayfish	0.04	6.66	8.80	0.57	0.76	0.46
Dragonflies	0.31	9.12	3.81	5.73	2.39	**0.03**
Mayflies	0.07	0.45	0.46	0.97	0.98	0.34
Snails	0.02	-1.22	2.49	0.24	-0.49	0.63
Total biomass	0.14	16.30	11.14	2.14	1.46	0.17

exposed shoreline reaches where fetch is short, while at long fetches the odds of lake sturgeon occupying exposed shoreline reaches increases almost threefold. In August, lake sturgeon were much less likely to occur on gentle littoral-zone slopes. Model subset "a" (a main-effects model; Table 10) shows that lake sturgeon in 2003 were more than twice as likely to occupy exposed over protected shorelines (Table 12), and they were 1.67

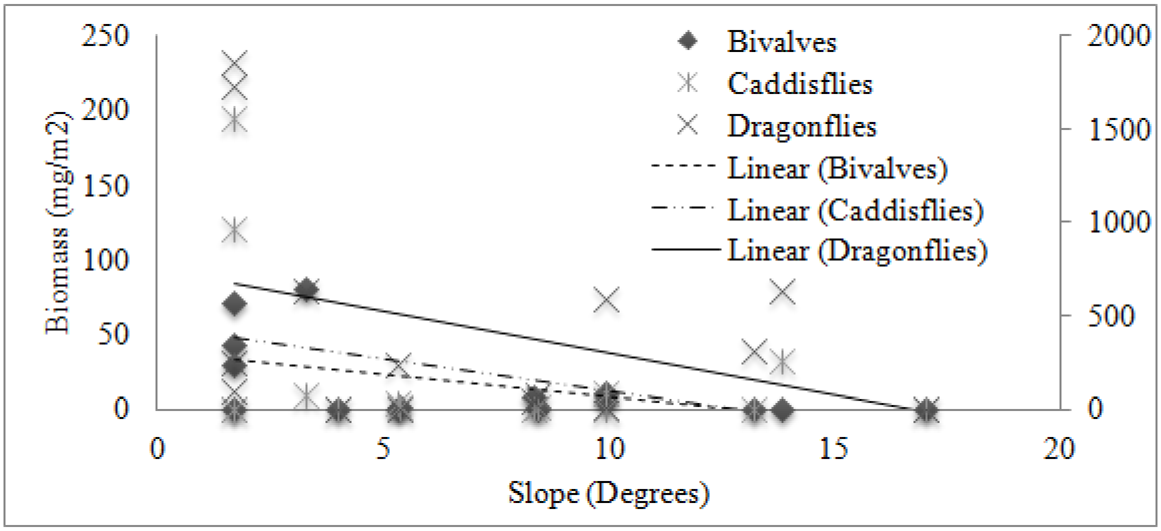

Figure 12. Significant linear relationships of invertebrate biomass with littoral-zone slope. Biomass of bivalves and caddisflies corresponds to the left axis; biomass of dragonflies corresponds to the right axis.

times more likely to occupy steep littoral-zone slopes overall (Table 10). Although not significant (*p* = 0.06), lake sturgeon were 1.57 times more likely to occupy shoreline reaches of short fetch in 2003 (Table 10 and 13). Model subset "b" (including the fetch and exposure interaction, but excluding a seasonal effect; Table 10) shows that fetch alone was not a significant predictor of lake sturgeon locations in 2003. Although not at significant levels, lake sturgeon locations in 2004 were twice as likely to be found at exposed shoreline reaches with short fetch (*p* = 0.06) and were less likely to be found on gentle slopes in august. (*p*=0.08; Table 14).

DISCUSSION

The unique premise of this study is that it relied on a set of coarse-scale, physical lake characteristics to describe communities of macroinvertebrate taxa, an approach sparsely referenced in other literature. More commonly, lake characteristics have been used to describe distribution of fish (Keast and Harker 1977; Randall et al. 1996), littoral-zone substrates (Herold et al. 2007), and aquatic macrophytes (Weisner et al. 1997; Brind'Amour et al. 2005). The comprehensive set of statistical analyses here provides a good insight into how coarse-scale, physical lake characteristics influence the Rainy Lake ecosystem.

On Rainy Lake, fetch, shoreline exposure and littoral-zone slope are all associated with differences in macroinvertebrate community structure and biomass. Invertebrates considered to be important to the lake sturgeon diet are part of dynamic communities that are also influenced by substrate type, macrophyte abundance and time of year. In particular, gentler littoral-zone slopes sheltered from the effects of wind and waves support finer substrates and a greater abundance of macrophytes, while shorelines with long fetch, large angles of exposure and steep littoral-zone slopes support coarser substrates where macrophytes are characteristically absent. These findings agree with predictions and show how benthic sediment types and macrophyte abundance are influenced by the coarse-scale physical lake characteristics as outlined by the first study objective. Randall et al. (1996) also found that macrophyte cover is reduced at shorelines with longer fetches, while areas of the Great Lakes with more macrophyte coverage are associated with finer substrates.

Total macroinvertebrate biomass, potentially the most important predictor of lake sturgeon feeding habitat, was higher in July and August on steep slopes, characteristic of rocky substrates. However, dragonflies and mayflies made up the majority of biomass along shoreline reaches with short fetch and gentle littoral-zone slopes, characteristic of finer substrates. Shoreline reaches with short fetch, steep littoral-zone slopes and high

Table 10. Significance of factors in three models describing lake sturgeon habitat selection based on telemetry locations during July and August, 2003. Fetch (0) = short fetch, exposure (0) = exposed, slope (0) = gentle, July (0) = August, and July (1) = July. Factors are indicated in boldface where $p < 0.05$.

Model	Factors	β	S.E.	95% Wald confidence interval		Wald Chi-square	Odds ratio		Odds ratio	*p*
				Lower	Upper		Lower	Upper		
a	Fetch (0)	0.45	0.23	-0.01	0.91	3.69	1.24	1.98	1.57	0.06
	Exposure (0)	0.79	0.25	0.31	1.27	10.37	1.73	2.82	2.21	**<0.01**
	Slope (1)	0.50	0.24	-0.97	-0.04	4.59	0.48	0.76	1.67	**0.03**
b	Fetch (0)	0.69	0.43	-0.16	-1.54	2.56	1.30	3.08	2.00	0.11
	Fetch (0) × exposure (0)	0.66	0.31	0.06	1.27	4.62	1.42	2.63	1.94	**0.03**
	Fetch (1) × exposure (0)	1.01	0.41	0.20	1.82	6.00	1.82	4.16	2.75	**0.01**
	Slope (1)	0.50	0.24	-0.97	-0.04	4.59	0.48	0.76	1.67	**0.03**
c	Fetch (0)	0.69	0.43	-0.16	-1.54	2.56	1.30	3.08	2.00	0.11
	Fetch (0) × exposure (0)	*0.66*	*0.31*	*0.06*	*1.27*	*4.62*	*1.42*	*2.63*	*1.94*	***0.03***
	Fetch (1) × exposure (0)	1.01	0.41	0.20	1.82	6.00	1.82	4.16	2.75	**0.01**
	July (0) × slope (0)	-1.06	0.39	-1.82	-0.30	7.52	1.96	4.25	0.35	**0.01**
	July (0) × slope (1)	0.17	0.29	-0.74	0.40	0.33	0.63	1.13	0.85	0.56
	July (1) × slope (0)	0.26	0.30	-0.85	0.32	0.78	0.57	1.04	0.77	0.38

Table 11. Frequency distributions of lake sturgeon locations in 2003 and 2004 according to littoral-zone slope, exposure and fetch during June, July and August.

	2003		2004	
Littoral-zone slope	Steep	Gentle	Steep	Gentle
June	n/a	n/a	1	6
July	26	20	14	13
August	22	9	17	13
Exposure	Exposed	Protected	Exposed	Protected
June	n/a	n/a	5	2
July	31	15	14	13
August	22	9	20	10
Fetch	Long	Short	Long	Short
June	n/a	n/a	4	3
July	19	27	10	17
August	11	20	17	13

exposure, as well as shorelines with short fetches, gentle littoral-zone slopes and good protection, provided habitat for dragonflies, likely corresponding to different communities among the nine dragonfly species found in the Rainy Lake area (McEwen and Butler 2008). Dragonfly biomass was higher in June than later in the summer, likely due to many species being in their final stages of development at that time. A second, upward trend in dragonfly biomass from July to August is likely due to growth of newly deposited eggs into newly sampled larval stages. Mayfly communities are an important component of the lake sturgeon diet before their emergence (Mosindy and Rusak 1991). Mayfly communities found at protected shorelines with gentle littoral-zone slopes and short fetch had a sharp decline later in the season compared to other mayfly communities, likely caused by a greater concentration of mayfly species with later emergence times. Across both sampling years, bivalves and caddisflies were found at short fetches. In 2010 caddisflies were most likely to be found at short fetches when the angle of exposure was

Table 12. Significance of factors in three models describing lake sturgeon habitat selection based on telemetry locations during June, July and August, 2004. Fetch (0) = short fetch, exposure (0) = exposed, slope (0) = gentle, July (0) = June or August, July (1) = July, August (0) = June or July, August (1) = August. Factors are indicated in boldface where $p < 0.05$.

Model	Factors	β	S.E.	95% Wald confidence interval		Wald Chi-square	Odds ratio		Odds ratio	*p*
				Lower	Upper		Lower	Upper		
a	Fetch (0)	0.06	0.25	-0.43	0.55	0.06	0.83	1.37	1.07	0.80
	Exposure (0)	0.45	0.26	-0.06	0.95	3.01	1.21	2.02	1.56	0.08
	Slope (0)	0.00	0.25	-0.49	0.49	0.00	0.78	1.28	1.00	1.00
b	Fetch (1)	0.24	0.40	-1.03	0.55	0.36	0.53	1.18	1.27	0.55
	Fetch(0) × exposure(0)	0.69	0.37	-0.03	1.42	3.52	1.38	2.89	2.00	0.06
	Fetch(1) × exposure(0)	0.19	0.36	-0.51	0.90	0.30	0.85	1.74	1.21	0.59
	Slope (0)	0.00	0.25	-0.49	0.49	0.00	0.78	1.28	1.00	1.00
c	Fetch (1)	0.24	0.40	-1.03	0.55	0.36	0.53	1.18	1.27	0.55
	Fetch(0) × exposure(0)	0.69	0.37	-0.03	1.42	3.52	1.38	2.89	2.00	0.06
	Fetch(1) × exposure(0)	0.19	0.36	-0.51	0.90	0.30	0.85	1.74	1.21	0.59
	July(0) × slope(0)	0.77	0.49	-1.74	0.19	2.45	0.28	0.76	0.46	0.12
	July(0) × slope(1)	2.64	1.04	-4.67	-0.61	6.50	0.03	0.20	0.07	**0.01**
	August(0) × slope(0)	2.91	1.10	-5.06	-0.75	7.00	0.02	0.16	0.05	**0.01**
	August(1) × slope(0)	2.13	1.20	-4.50	0.23	3.14	0.04	0.39	0.12	0.08
	August(0) × slope(1)	2.83	1.03	-4.85	-0.82	7.58	0.02	0.16	0.06	**0.01**

large, while in 2011 caddisflies had lower abundance at larger angles of exposure. Although not in June, bivalves were mainly found on gentle slopes. Their absence in June may be due to individuals not yet having moved into the littoral zone from greater depths. On rocky habitats, snail biomass was higher in July than in June and higher again in August along most shoreline reaches. Growth of individual snails and upward migration of snails from greater depths into the littoral zone may be explanations. Later in August, snails dominated rocky and exposed shoreline reaches with steep slopes, characteristic of rocky points in Rainy Lake. Similarities in the occurrence of most macroinvertebrates between years suggest that habitat selection patterns for macroinvertebrates are relatively constant temporally.

Evidence of optimal foraging was identified by comparing shoreline reaches where preferred prey items were found to the actual lake sturgeon telemetry locations. Lake sturgeon locate along shoreline reaches with highest prey biomass and respond in frequency of locations to the seasonally dynamic prey base. Despite having relatively imprecise sturgeon locations and a small sample size in June, examination of feeding habitats in 2003 and 2004 was possible. Relationships may have been stronger between the macroinvertebrate communities and lake sturgeon locations if there was a smaller span of years between the collection of lake sturgeon locations in 2003 and 2004 and collection of macroinvertebrate biomass data in 2010 and 2011, during which time physical and biological changes could have occurred in the system. Some lake sturgeon locations may represent migrating to other feeding habitats instead of actually feeding. Regardless, the best-fit model based on macroinvertebrate biomass shows lake sturgeon preference for exposed shoreline reaches with long fetch and steep slopes in August. Total macroinvertebrate biomass is higher in July and August on steeper littoral-zone slopes, comprising primarily snails and crayfish biomass. In June, exposed shoreline reaches with gentler slopes and short fetches with communities of mayflies and dragonflies seem to be the plausible location for lake sturgeon feeding. Lake sturgeon locations also indicate a switch from shorelines abundant in dragonfly and mayfly communities in June to sites of increased snails and crayfish biomasses in July and August. Research involving stomach analysis would be a means to confirm this habitat switch. Similar to this study, Brind'Amour et al. (2005) found large differences in fish communities between June and August, while fetch and emergent macrophytes were the most important variables in describing their habitats. Keast and Harker (1977) also found that fish and invertebrate distributions are highly correlated, such that the higher presence of fish in the shallows is associated with greater benthic invertebrate biomass.

Continued research on how macroinvertebrate communities respond to lake characteristics that can be remotely sensed could develop an efficient tool, saving countless hours of fieldwork investigating macroinvertebrate communities or habitat of benthic-feeding fish. Research involving coarse-scale, physical lake characteristics could also be paired with relatively precise information increasingly available on substrate types or macrophyte coverage from remote sensing.

LITERATURE CITED

Adams, W.E., L.W. Kallemeyn and D.W. Willis. 2006a. Lake sturgeon population characteristics in Rainy Lake, Minnesota and Ontario. J. Appl. Ichthyol. 22: 97-102.

Adams, W.E., L.W. Kallemeyn and D.W. Willis. 2006b. Lake sturgeon, *Acipenser fulvescens*, movements in Rainy Lake, Minnesota and Ontario. Can. Field-Nat. 120: 71-82.

Auer, N.A. 1996. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can. J. Fish. Aquat. Sci. 53: 152-160.

Beamish, F.W.H, D.L.G. Noakes and A. Rossiter. 1998. Feeding ecology of juvenile lake sturgeon, *Acipenser fulvescens*, in northern Ontario. Can. Field-Nat. 112(3): 459-468.

Brind'Amour, A., D. Boisclair, P. Legendre and D. Borcard. 2005. Multiscale spatial distribution of a littoral fish community in relation to environmental variables. Limnol. Oceanogr. 50: 465-479.

Burnham, K.P. and D.R. Anderson. 2002. Model Selection and Multimodel Inference. Springer Science and Business Media, Inc. New York, NY. 488 pp.

Chiasson, W.B., D.L.G Noakes and F.W.W.H. Beamish. 1997. Habitat, benthic prey, and distribution of juvenile lake sturgeon (*Acipenser fulvescens*) in northern Ontario rivers. Can. J. Fish. Aquat. Sci. 54: 2866-2871.

COSEWIC 2000. COSEWIC assessment and update status report on the lake sturgeon *Acipenser fulvescens* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. Xi + 107 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

Covich, A.P., M.A. Palmer and T.A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems. BioScience 49: 119-127.

Downing, J.A. and F.H. Rigler (eds.). 1984. A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications. Oxford, England. 500 pp.

Fortin, R. P. Dumont, S. Guénette 1996. Determinants of growth and body condition of lake sturgeon (*Acipenser fulvescens*). Can. J. Fish. Aquat. Sci. 53: 1150-1156.

Halliday, W.D. 2010. What habitats do foraging lake sturgeon select in Rainy Lake? HBSc thesis, Dept. Biology, Lakehead University.

Harkness, W.J.K. and J.R. Dymond. 1961. The lake sturgeon. Ontario Dept. Lands and Forests, Fish and Wildlife Branch. Toronto, ON. 97 pp.

Haxton, T.J. and C.S. Findlay. 2008. Variation in lake sturgeon (*Acipenser fulvescens*) abundance and growth among river reaches in a large regulated river. Can. J. Fish. Aquat. Sci. 65: 645-657.

Haxton, T.J., C.S. Findlay and R.W. Threader. 2008. Predictive value of a lake sturgeon habitat suitability model. N. Amer. J. Fish. Manage. 28: 1373-1383.

Herold, M., J. Metz and J. S. Romsos. 2007. Inferring littoral substrates, fish habitats, and fish dynamics of Lake Tahoe using IKONOS data. Can. J. Remote Sensing, 33: 445-456.

Holey M.E. and T.N. Trudeau. 2005. The state of Lake Michigan in 2000. Great Lakes Fisheries Commission Spec. Publ. 05-01.

Jackson, R.J., A.J. VanDeValk, T.E. Brooking, O.A. VanKeeken and L.G. Rudstam. 2002. Growth and feeding dynamics of lake sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York: results from the first five years of a restoration program. J. Appl. Ichthyol. 18: 439-443.

Jones, C., K.M. Somers, B. Craig and T.B. Reynoldson. 2004. Ontario benthos biomonitoring network protocol manual. Ont. Min. Environ., Dorset, ON. 107 pp.

Kallemeyn, L. W., K.L. Holmberg, J.A. Perry and B.Y. Odde. 2003. Aquatic synthesis for Voyageurs National Park. US Geol. Surv. Info. Tech. Rep. 2003-0001.

Keast, A. and J. Harker. 1977. Fish distribution and benthic invertebrate biomass relative to depth in an Ontario lake. Env. Biol. Fish. 2: 235-240.

Leonard, N.J., W.W. Taylor and C. Goddard. 2004. Multijurisdictional management of lake sturgeon in the Great Lakes and St. Lawrence River. In: G.T.O. LeBreton, F.W.H. Beamish and R.S. McKinley (eds.) Sturgeons and Paddlefish of North America, Kluwer Academic Publishers. pp. 231-251.

Magnin, E. 1966. Recherches sur les cycles de reproduction des sturgeons *Acipenser fulvescens* Rafinesque. Ann. Stat. Centr. Hydrobiol. Appl. 9: 8-242.

Manny, B.A. and G.W. Kennedy. 2002. Known lake sturgeon (*Acipenser fulvescens*) spawning habitat in the channel between lakes Huron and Erie in the Laurentian Great Lakes. J. Appl. Ichthyol. 18: 486-490.

McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon. 300 pp.

McEwen, D.C. and M.G. Butler. 2008. Impacts from water level regulation on benthic macroinvertebrate community structure in Namakan Reservior and Rainy Lake: Voyageurs National Park. Natural Resource Technical Report NPS/NRPC/WRD/NRTR-2008/129. National Park Service, Fort Collins Colorado.

Mosindy, T. and J. Rusak. 1991. An assessment of lake sturgeon populations in Lake of the Woods and the Rainy River, 1987-90. Lake of the Woods Fisheries Assessment Unit. OMNR. Report 1991-01.

Peckarsky, B.L., P.R. Fraissinet, M.A. Penton and D.J. Conklin, Jr. 1990. Freshwater Macroinvertebrates of Northeastern North America. Cornell University Press, Ithaca, NY. 442 pp.

Peterson, D.L., P. Vecsei and C.A. Jennings. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fisheries 17: 59-76.

Randall, R.G., C.K. Minns, V.W. Cairns and J.E. Moore. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Can. J. Fish. Aquat. Sci. 53: 35-44

Rosenberg, D.M., I.J. Davies, D.G. Cobb and A.P. Wiens. 2001. Protocols for Measuring Biodiversity: Benthic Macroinvertebrates in Fresh Waters. Environment Canada. http://www.eman-rese.ca/eman/ecotools/protocols/freshwater/benthics/introduc.html. April 19, 2010.

Roussow, G. 1957. Some considerations concerning sturgeon spawning periodicity. J. Fish. Res. Board Canada 14: 553-572.

Seyler, John. 1997. Adult lake sturgeon (*Acipenser fulvescens*) habitat use, Groundhog River 1996. OMNR, Northeast Science & Technology. Timmins, Ontario. TR-035. 28 pp.

SPSS. 2007. SPSS Base 16.0 User’s Guide. SPSS Inc. 233 South Wacker Drive, 11th Floor, Chicago IL 60606-6412.

Thorp, J.H. and A.P. Covich. 1991. Ecology and Classification of North American Freshwater Invertebrates. Academic Press. San Diego, California. 911 pp.

Threader, R.W., R.J. Pope and P.R.H. Schaap. 1998. Development of a Habitat Suitability Index Model for Lake Sturgeon (*Acipenser fulvescens*). Hydroelectric, Ontario Hydro. Rept, No: H-07015.01-0012. 151 pp.

Vecsei, P. and D. Peterson. 2005. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers. pp. 103-133.

Weisner, S.E.B., J.A. Strand and H Sandsten. 1997. Mechanisms regulating abundance of submerged vegetation in shallow eutrophic lakes. Oecologia 109: 592-599.

Werner, R.G. and J. Hayes. 2005. Contributing factors in habitat selection by lake sturgeon (*Acipenser fulvescens*). Unites States Environmental Protection Agency-Great Lakes National Program Office: GL97517201. 24 pp.

Wilson, J.A. and R.S. McKinley. 2004. Sturgeons and Paddlefish of North America. Kluwer Academic Publishers. pp. 40-72.

Witzel, R.G. 2007. Limnology Lake and River Ecosystems. Third Edition. Academic Press. San Diego, California. 1006 pp.