RAINBOW AND MIDDLE LAKES-LAKE IMPROVEMENT BOARD FALL 2010 PROGRESS REPORT

Conducted pursuant to
PA 451 of 1994 as amended,
and the rules promulgated thereunder

***Prepared for*:**
Rainbow and Middle Lakes-Lake Improvement Board
Montcalm County, Michigan

TABLE OF CONTENTS

FIGURES

FIGURE **PAGE**

TABLES

I. EXECUTIVE SUMMARY

Rainbow Lake is a 168-acre, natural lake located in section 19 and 20 of Pine Township in Montcalm County, Michigan (T. 11N, R. 8W). The maximum depth of the lake is 22.0 feet and the average (mean) depth is 5.0 feet. The lake contains 3.1 miles of shoreline and has a fetch (longest distance across the lake) of approximately 0.97 miles (MDNRE, 2009), which may yield sizeable waves during high winds. Recent limnological surveys of the lake indicate that the lake is meso-eutrophic, with high Secchi disk transparency, elevated nutrients such as nitrogen and phosphorus, and exotic and native aquatic macrophyte growth. Middle Lake is a 37-acre, natural lake located in sections 20 and 29 of Pine Township in Montcalm County, Michigan (T. 11N, R. 8W) and contains 0.96 miles of shoreline and has a fetch (longest distance across the lake) of approximately 0.33 miles (MDNRE, 2010).

Eurasian Watermilfoil (*Myriophyllum spicatum*; Figure 1) was introduced to the United States in the 1950's and has spread to many of Michigan's inland lakes. Currently, it exists in over 33 of the United States. Lakes with moderate to high water transparency and public access sites (such as Elizabeth Lake) are most vulnerable to Eurasian Watermilfoil infestation. Eurasian Watermilfoil is among the first species to germinate in lakes during the spring, and quickly forms a dense surface canopy that impedes the necessary light for more favorable, native aquatic plant species. Eurasian Watermilfoil reproduces by seed and fragmentation and may even hybridize with native milfoil species if present in the lake. It is also capable of overwintering under winter ice, although a fair amount of the previous seasonal vegetation does decay. The previously observed Eurasian Watermilfoil population in Rainbow and Middle Lakes was of great concern due to the negative impacts it had on native aquatic plant biodiversity, which ultimately impacts the fishery and the overall balance of the lake. Curly-Leaf Pondweed (*Potamogeton crispus*) is an exotic pondweed with reddish midveins and wavy leaf margins (Figure 2). It forms turions later in the season that are deposited to the sediments if not treated or removed. Although the plant forms dense canopies when in large quantities, it does die back naturally by late summer. Rigorous lake management approaches such as the use of systemic herbicides used in July of 2010 to control Eurasian Watermilfoil and Curly-Leaf Pondweed in both lakes were successfully implemented.

Figure 1. Eurasian milfoil (*Myriophyllum spicatum L.*) with lateral branches and seed head. © *Superior Photique, 2007.*

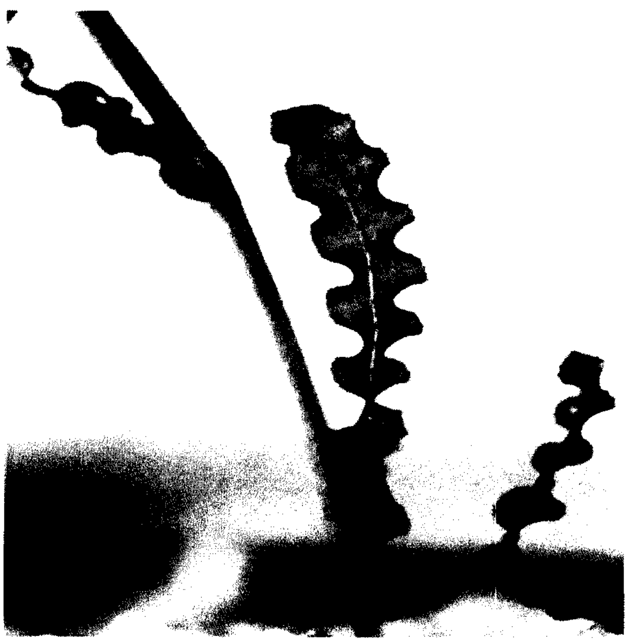


Figure 2. Curly-Leaf Pondweed (*Potamogeton crispus*) with wavy leaf margins and red midveins in leaves. © *Superior Photique, 2007.*

Watershed inputs of nutrients through road and impervious surface runoff, lawn fertilizers, and storm drains may be contributing excess nutrients to Rainbow and Middle Lakes. In particular, the north shore of Middle Lake may be influenced by road runoff, where as the southwest shore may be influenced by agricultural runoff, although an adequate forest buffer appears to be adequate for removal of substances prior to entry into the lake. The northwest corner of Rainbow Lake lacks an adequate forest buffer between the agricultural land and the lake and thus implementation of an adequate buffer at this location should be considered. Excessive nutrients both saturate the sediment and water column of the lake and act as continual sources for emergent and submersed macrophytes. A smaller watershed has fewer opportunities for pollution; however, it is critical to monitor land uses within the immediate watershed to target any potential pollutant inputs. Watershed management plan strategies which implement BMP's are needed to ensure long-term improvement of the lake. These BMP's will continue to be presented to the riparians in educational newsletters.

In summary, lake improvement strategies for Rainbow and Middle Lakes should include both within-lake and watershed components. Cooperation among the riparian residents and the township is critical for success of the lake management program.

II. RAINBOW AND MIDDLE LAKES IMPROVEMENT STRATEGIES-

A. Aquatic Herbicides and Algaecides

Aquatic herbicides are an effective method for the control of nuisance native and exotic macrophytes. The Natural Resources and Environmental Protection Act, P.A. 451 of 1994 (Part 33) mandates that a permit be acquired from the Michigan Department of Natural Resources and Environment prior to all aquatic herbicide treatments. There are two broad categories of aquatic herbicides; Contact and Systemic. Systemic herbicides can be applied to various areas or to an entire system and kill the entire plant. In contrast, contact herbicides kill only the shoot portion of the plant. Algaecides also fall into the herbicide category and are effective on all types of algae including filamentous (surface), planktonic (submersed), and periphytic (submersed on aquatic plants) forms. The continued use of systemic aquatic herbicides such as 2,4-D and

Triclopyr OTF for the control of Eurasian Watermilfoil and the use of Aquathol-K for Curly-leaf Pondweed in Rainbow and Middle Lakes is recommended to achieve good results over a long-term period. At this time, a whole-lake (fluridone) treatment is not recommended, as there is not enough Eurasian Watermilfoil to qualify for that permit.

B. Aquatic Vegetation and Algal Composition Surveys

Aquatic vegetation communities are dynamic and are composed of plants with different structural architecture. Most aquatic systems contain floating-leaved, submersed, and emergent aquatic macrophytes. These differences in aquatic plant structure enhance biodiversity of macroinvertebrates in the lake and thus offer a more diverse food source for the fishery. Repeated vegetation surveys of the lake are critical for documenting the changes in ecosystem structure that will vary with changes in water levels, nutrient concentrations, and aquatic plant control activities. Furthermore, systems such as Rainbow and Middle Lakes which are infested with exotic macrophytes such as Eurasian Watermilfoil and Curly-leaf Pondweed, require frequent monitoring to evaluate the progress of the selected management techniques. A spring pre-treatment and late summer post-treatment and final AVAS/GPS inventory survey were conducted on May 27 and August 27 of 2010, respectively and will be conducted again in 2011. The initial treatment occurred on July 7, 2010 and was preceded by a survey on July 2, 2010. The recent AVAS/GPS grid survey conducted on Rainbow and Middle Lakes on August 27, 2010 revealed the presence of 2 exotic species (Table 1), including Eurasian Watermilfoil, and Curly-leaf Pondweed. The survey also detected 13 native submersed species, 1 floating-leaved and 3 emergent species for a total of 17 species (Table 2). There were many pondweeds found in the lakes, which resemble the entire-leaved structure in Figure 3.

Macrophyte Species and Code	***Common Name***	***Plant Growth Form***
Myriophyllum spicatum, 1	Eurasian Watermilfoil	Submersed; Rooted
Potamogeton crispus, 2	Curly-leaf Pondweed	Submersed; Rooted

Table 1. Exotic aquatic macrophyte species found in and around Rainbow and Middle Lakes (August 27, 2010)

Macrophyte Species and Code	***Common Name***	***Plant Growth Form***	***Relative Density***
Chara vulgaris (macroalga), 3	Muskgrass	Submersed; Rooted	Common
Stuckenia pectinatus, 4	Sago Pondweed	Submersed; Rooted	Common
Potamogeton zosteriformis, 5	Flatstem Pondweed	Submersed; Rooted	Sparse
Potamogeton gramineus, 7	Variable-leaved Pondweed	Submersed; Rooted	Sparse
Potamogeton praelongus, 8	White-stemmed Pondweed	Submersed; Rooted	Common
Potamogeton richardsonii, 9	Richardson's Pondweed	Submersed; Rooted	Common
Potamogeton illinoensis, 10	Illinois Pondweed	Submersed; Rooted	Common
Potamogeton amplifolius, 11	Large-leaf Pondweed	Submersed; Rooted	Sparse
Potamogeton pusillus, 29	Small-leaf Pondweed	Submersed: Rooted	Sparse
Heteranthera dubia, 14	Water Stargrass	Submersed; Rooted	Sparse
Elodea canadensis, 21	Common Waterweed	Submersed; Rooted	Sparse
Ceratophyllum demersum, 20	Coontail	Submersed; Non-rooted	Sparse
Najas guadalupensis, 25	Southern Naiad	Submersed; Rooted	Sparse
Eleocharis acicularis, 27	Spikerush	Emergent	Sparse
Nymphaea odorata, 30	White Waterlily	Floating-Leaved	Common
Typha latifolia, 39	Cattails	Emergent	Sparse/Common
Decadon verticillatus, 42	Swamp Loosestrife	Emergent	Sparse/Common

Table 2. Native aquatic macrophyte species found in and around Rainbow and Middle Lakes (May 27, July 2, and August 27, 2010).

Phytoplankton (Algae Analysis)-

In addition to the aquatic vegetation analyses, algal community composition was assessed as a composite sample from the deep basins of Rainbow and Middle Lakes. Algal genera from composite water samples collected over the Deep Basin of the lakes in August of 2010 were analyzed under a compound brightfield microscope. The genera present included the Chlorophyta (green algae): *Chlorella* sp., *Scenedesmus* sp., *Euglena* sp., *Spirogyra* sp., *Synechococcus* sp., *Gleocystis* sp., *Pandorina* sp., *Zygnema* sp., *Protococcus* sp., *Haematococcus* sp., *Pediastrum* sp., *Cryptomonas* sp., *Closterium* sp., *Chloromonas* sp., *Ulothrix* sp., *Rhizoclonium* sp., and *Mougeotia* sp., The Cyanophyta (blue-green algae): *Gleocapsa* sp., *Anabaena* sp., *Microcystis* sp., and *Oscillatoria* sp.; The Bascillariophyta (diatoms) *Navicula* sp., *Synedra* sp., *Asterionella* sp., *Stephanodiscus* sp., *Fragilaria* sp., *Cymbella* sp., *Nitzschia* sp., and *Tabellaria* sp. The aforementioned species indicate a diverse algal flora and represent a relatively balanced freshwater ecosystem, capable of supporting a healthy zooplankton community in favorable water quality conditions. Blue-green algae such as *Microcystis* sp., and *Oscillatoria* sp., are capable of producing microtoxins (Rinehart et al. 1994) that can cause neurologic or hepatic (liver) dysfunction in animals or humans if ingested in large quantities. Blue-green blooms are usually visible as a bluish tinted surface "scum layer" on lake waters when they are a threat and these areas should be avoided when obvious surface layer blooms are present. The waters of Rainbow and Middle Lakes are rich in the Chlorophyta (both filamentous and planktonic green algae), which are indicators of good water quality and also support a robust fishery.

C. Water Quality Monitoring of Rainbow and Middle Lakes

The quality of water is highly variable among Michigan inland lakes, although some characteristics are common among particular lake classification types. The water quality of Rainbow and Middle Lakes is affected by both land use practices and climatic events. Climatic factors (i.e. spring runoff, heavy rainfall) may alter water quality in the short term; whereas, anthropogenic (man-induced) factors (i.e. shoreline development, lawn fertilizer use) alter water quality over longer time periods. Furthermore, lake water quality helps to determine the classification of particular lakes (Table 3). Lakes that are high in nutrients (such as phosphorus and nitrogen) and chlorophyll-*a*, and low in transparency are classified as **eutrophic**; whereas those that are low in nutrients and chlorophyll-*a*, and high in transparency are classified as **oligotrophic**. Lakes that fall in between these two categories are classified as **mesotrophic**. Rainbow and Middle Lakes may be classified as meso-eutrophic based on their high transparency and moderate nutrient concentrations.

Lake Trophic Status	*Total Phosphorus ($\mu g\ L^{-1}$)*	*Chlorophyll-a ($\mu g\ L^{-1}$)*	*Secchi Transparency (feet)*
Oligotrophic	< 10.0	< 2.2	> 15.0
Mesotrophic	10.0 – 20.0	2.2 – 6.0	7.5 – 15.0
Eutrophic	> 20.0	> 6.0	< 7.5

Table 3. Lake Trophic Status Classification Table (MDNRE)

Rainbow and Middle Lakes Water Quality Parameters

Water quality parameters such as dissolved oxygen, water temperature, conductivity, turbidity, total dissolved solids, pH, total alkalinity, total phosphorus, total Kjeldahl nitrogen, and Secchi transparency, among others, all respond to changes in water quality and consequently serve as indicators of water quality change. These parameters are discussed below along with water quality data specific to Rainbow and Middle Lakes which was collected on August 27, 2010 (Tables 4 and 5).

Dissolved Oxygen

Dissolved oxygen is a measure of the amount of oxygen that exists in the water column. In general, dissolved oxygen levels should be greater than 5 mg L^{-1} to sustain a healthy warm-water fishery. Dissolved oxygen concentrations in the lakes may decline if there is a high biochemical oxygen demand (BOD) where organismal consumption of oxygen is high due to respiration. Dissolved oxygen is generally higher in colder waters. Dissolved oxygen is measured in milligrams per liter (mg L^{-1}) with the use of a dissolved oxygen meter and/or through the use of Winkler titration methods. The dissolved oxygen concentrations in Rainbow Lake were normal and ranged between 8.9 mg L^{-1} at the surface and 0.5 mg L^{-1} at the bottom. During summer months, dissolved oxygen at the surface is generally higher, due to the exchange of oxygen from the atmosphere with the lake surface, whereas dissolved oxygen is lower at the lake bottom due to decreased contact with the atmosphere and increased biochemical oxygen demand (BOD) from microbial activity. A decline in dissolved oxygen may cause increased release rates of phosphorus (P) from the Rainbow Lake bottom sediments if dissolved oxygen levels drop to near zero milligrams per liter. Late summer dissolved oxygen concentrations ranged from 9.0 mg L^{-1} at the surface to 0.7 mg L^{-1} at the bottom in Middle Lake due to increased biochemical oxygen demand at the lake bottom.

Water Temperature

The water temperature of lakes varies within and among seasons and is nearly uniform with depth under winter ice cover because lake mixing is reduced when waters are not exposed to wind. When the upper layers of water begin to warm in the spring after ice-off, the colder, dense layers remain at the bottom. This process results in a "thermocline" that acts as a transition layer between warmer and colder water layers. During the fall season, the upper layers begin to cool and become denser than the warmer layers, causing an inversion known as "fall turnover". In general, lakes with deep basins will stratify and experience turnover cycles. Water temperature is measured in degrees Celsius (°C) or degrees Fahrenheit (°F) with the use of a submersible thermometer. The summer water temperatures of Rainbow Lake demonstrated a thermocline between the surface and a "middle depth" of 19 feet, since the lake was sampled during a thermally stratified period. Water temperatures for Rainbow Lake ranged between 83.4°F at the surface and 71.5 °F at the lake bottom. Water temperatures for Middle Lake ranged between 84.2°F at the surface and 71.9 °F at the lake bottom. Due to the significantly higher water temperatures during the summer of 2010 than in previous years, many aquatic plants were able to colonize at greater depths and the dissolved oxygen concentrations throughout the lakes were slightly lower since warmer waters hold less oxygen than cooler waters.

Conductivity

Conductivity is a measure of the amount of mineral ions present in the water, especially those of salts and other dissolved inorganic substances. Conductivity generally increases as the amount of dissolved minerals and salts in a lake increases, and also increases as water temperature increases. Conductivity is measured in microsiemens per centimeter ($\mu S\ cm^{-1}$) with the use of a conductivity probe and meter. Conductivity values for the lakes were moderate and similar to most healthy inland lakes in Michigan. Conductivity ranged between 282 μmho cm^{-1} and 310 $\mu S\ cm^{-1}$ for both lakes.

Turbidity

Turbidity is a measure of the loss of water transparency due to the presence of suspended particles. The turbidity of water increases as the number of total suspended particles increases. Turbidity may be caused from erosion inputs, phytoplankton blooms, stormwater discharge, urban runoff, re-suspension of bottom sediments, and by large bottom-feeding fish such as carp. Particles suspended in the water column absorb heat from the sun and raise the water temperature. Since higher water temperatures generally hold less oxygen, shallow turbid waters are usually lower in dissolved oxygen. Turbidity is measured in Nephelometric Turbidity Units (NTU's) with the use of a turbimeter. The World Health Organization (WHO) requires that drinking water be less than 5 NTU's; however, recreational waters may be significantly higher than that. The turbidity of both lakes was low and ranged from 0.2 – 1.4 NTU's during the sampling event. The lake bottom is predominately sandy substrate with some silt, which increases the turbidity values near the lake bottom.

pH

pH is the measure of acidity or basicity of water. The standard pH scale ranges from 0 (acidic) to 14 (alkaline), with neutral values around 7. Most Michigan lakes have pH values that range from 6.5 to 9.5. Acidic lakes (pH < 7) are rare in Michigan and are most sensitive to inputs of acidic substances due to a low acid neutralizing capacity (ANC). pH is measured with a pH electrode and pH-meter in Standard Units (S.U). The pH of Rainbow and Middle Lakes water ranged from 7.9 – 8.5 during the late summer sampling. From a limnological perspective, both lakes are considered "slightly basic" on the pH scale.

Total Alkalinity

Total alkalinity is the measure of the pH-buffering capacity of lake water. Lakes with high alkalinity (> 150 mg L^{-1} of $CaCO_3$) are able to tolerate larger acid inputs with less change in water column pH. Many Michigan lakes contain high concentrations of $CaCO_3$ and are categorized as having "hard" water. Total alkalinity is measured in milligrams per liter of $CaCO_3$ through an acid titration method. The total alkalinity of Rainbow and Middle Lakes is considered "moderate" (< 150 mg L^{-1} of $CaCO_3$), and indicates that the water is not hard or highly alkaline. Total alkalinity ranged from 96 - 121 mg L^{-1} of $CaCO_3$ during the late summer sampling. Total alkalinity may change on a daily basis due to the re-suspension of sedimentary deposits in the water and respond to seasonal changes due to the cyclic turnover of the lake water.

Oxidative Reduction Potential

The oxidation reduction potential of water describes the effectiveness of certain atoms to serve as potential oxidizers and indicates the degree of reductants present within the water. In general, the Eh level (measured in millivolts) decreases in anoxic (low oxygen) waters. Low E_h values are therefore indicative of reducing environments where sulfates (if present in the lake water) may be reduced to hydrogen sulfide (H_2S). Decomposition by microorganisms in the bottom water layers may also cause the E_h value to decline with depth. The E_h (ORP) values for the Rainbow Lake ranged between 67.8 mV and 33.9 mV, which are within a normal range for inland lakes. ORP values for Middle Lake ranged between 54.6 mV and 29.6 mV which is also a normal value for inland lakes.

Secchi Transparency

Secchi transparency is a measure of the clarity or transparency of lake water, and is measured with the use of an 8-inch diameter standardized Secchi disk. Secchi disk transparency is measured in feet (ft) or meters (m) by lowering the disk over the shaded side of a boat around noon and taking the mean of the measurements of disappearance and reappearance of the disk. Elevated Secchi transparency readings allow for more aquatic plant and algae growth. Eutrophic systems generally have Secchi disk transparency measurements less than 7.5 feet due to turbidity caused by excessive planktonic algae growth. The Secchi transparency of Rainbow Lake and Middle Lake averaged 13.0

feet and 12.5 feet, over the deep basin, respectively. This transparency is adequate to allow abundant growth of algae and aquatic plants in the majority of the littoral zone of the lakes. Secchi transparency is variable and depends on the amount of suspended particles in the water (often due to windy conditions of lake water mixing) and the amount of sunlight present at the time of measurement.

Depth ft	*Water Temp °F*	*DO mg L^{-1}*	*pH S.U.*	*Cond. µmho cm^{-1}*	*Turb. NTU*	*ORP mV*	*Total Alkalinity mgL^{-1} $CaCO_3$*
0	83.4	8.9	8.5	282	0.3	67.8	121
10	79.8	6.9	8.4	289	0.4	66.2	118
21	71.5	0.5	7.7	310	0.8	33.9	98

Table 4. Rainbow Lake water quality parameter data collected on August 27, 2010.

Depth ft	*Water Temp °F*	*DO mg L^{-1}*	*pH S.U.*	*Cond. µmho cm^{-1}*	*Turb. NTU*	*ORP mV*	*Total Alkalinity mgL^{-1} $CaCO_3$*
0	84.2	9.0	8.5	286	0.2	54.6	124
10	77.1	7.0	8.1	301	0.9	51.3	110
22	71.9	0.7	7.9	307	1.4	29.6	96

Table 5. Middle Lake water quality parameter data collected on August 27, 2010.

D. *Watershed Management Education and Implementation*

Many point and non-point sources are responsible for nutrient loads to aquatic systems. In addition, many residential lawns are regularly enriched with fertilizers that contain P. Many counties within Michigan are introducing P bans and P-free fertilizers and dishwashing detergents are becoming more available. Storm drains may also contribute nutrients to aquatic systems; however, if nutrient sources are dramatically reduced in proximity to the drains, the effluent is generally not nutrient-enriched and not a threat to the system. Riparian zone (shoreline) vegetation should also be preserved to act as a filter of nutrients that originate in the watershed and eventually enter the lake. Both lakes contain an ample amount of riparian vegetation which regulates nutrients with the high degree of agricultural lands around the lake. A detailed soils map showing the soil types around both lakes can be found in Appendix A. In summary, the east shore of Rainbow Lake contains a high amount of McBride and Isabella Sandy Loams (Mm) and the west shore contains an abundance of Montcalm Loamy Sand (Mt) and Sandy Loams both at 6-10% slopes. Erosion risk on these soils is moderate and thus riparian buffers on the shore and agricultural/forest buffers between crop land and the residential areas should be encouraged. Both of these soil types are not prone to ponding. However, soils with the code of (Ra) are Rifle and Tawas Peats and are prone to ponding. These soil types may be found at various locations around the shoreline of Rainbow Lake.

The dominant soils around Middle Lake include Montcalm and McBride Loamy Sands (Mw) on the west sore and Montcalm and McBride Loamy Sands (Mx) on the east and south shores, both with a range of 0-6% slopes. Erosion is less of a risk in these locations in comparison to those of Rainbow Lake. The southwest and southeast corners of Middle Lake also contain (Ra) which are Rifle and Tawas Peats and are prone to ponding. In areas where ponding may be prevalent, the elimination of goose droppings or other bacteria or nutrient sources should be implemented to reduce the entry of these substances to Middle and Rainbow Lakes.

III. RAINBOW AND MIDDLE LAKES PROPOSED 2010 LAKE IMPROVEMENT BUDGET

A proposed budget for the 2011 season of the Rainbow and Middle Lakes Improvement Program is shown below in Table 6.

2011 Proposed Rainbow and Middle Lakes Management Budget

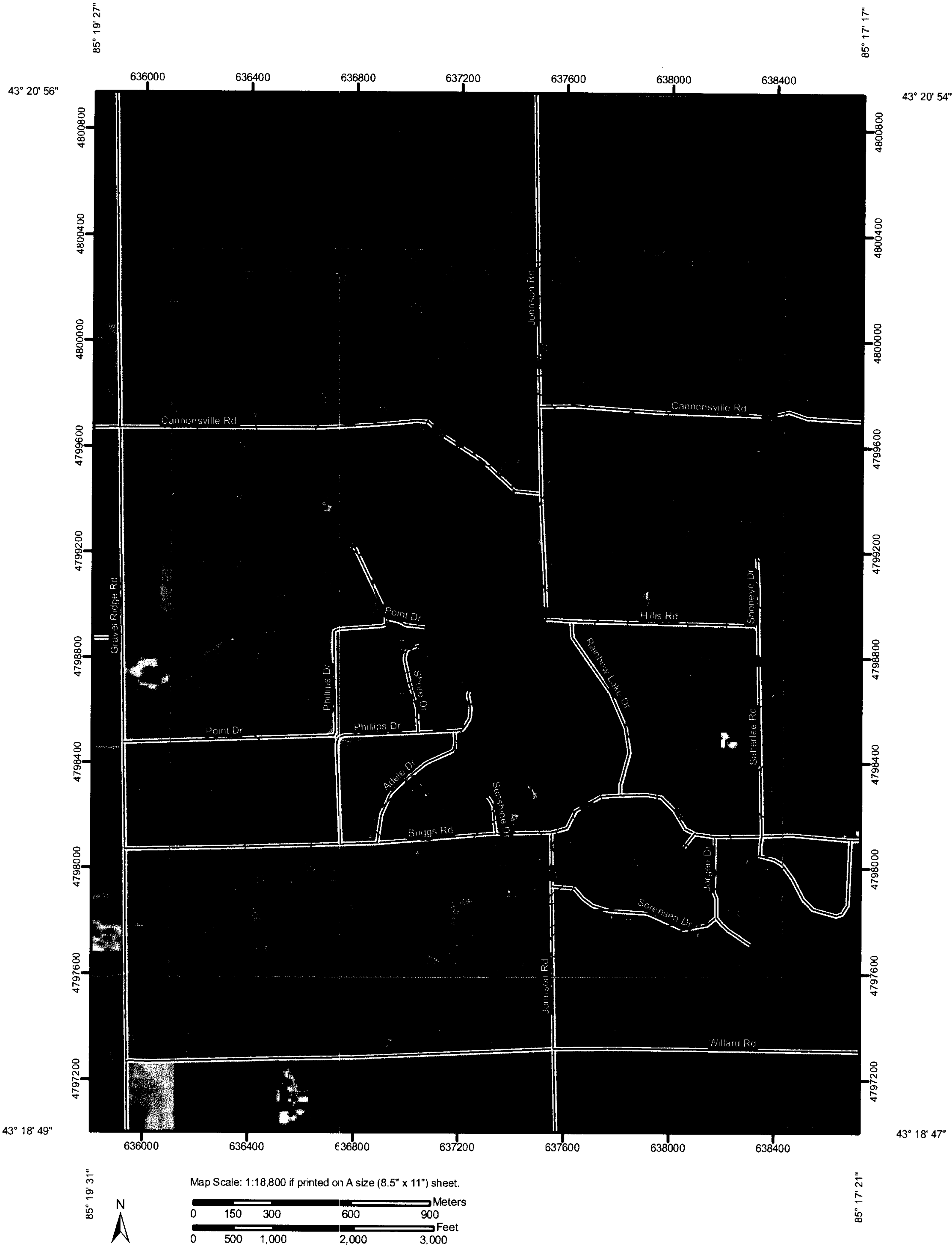
Improvement Strategy	Estimated Cost
Aquatic Herbicide Treatments (35 acres@$490 per acre)	$23,800
(15 acres@$390 per acre + MDNRE permit)	
Consulting Fees	$4,500
(Administration, surveys, sampling)	
Contingency (10%)	$2,830
Total 2011 Estimated Program Cost	$31,130

Table 6. Rainbow and Middle Lakes proposed lake management costs for 2011.

APPENDIX A

RAINBOW AND MIDDLE LAKES SHORELINE SOILS

Soil Map—Montcalm County, Michigan
(Rainbow and Middle Lakes Shoreline Soils)



MAP LEGEND

Area of Interest (AOI)

- Area of Interest (AOI)

Soils

- Soil Map Units

Special Point Features

- Blowout
- Borrow Pit
- Clay Spot
- Closed Depression
- Gravel Pit
- Gravelly Spot
- Landfill
- Lava Flow
- Marsh or swamp
- Mine or Quarry
- Miscellaneous Water
- Perennial Water
- Rock Outcrop
- Saline Spot
- Sandy Spot
- Severely Eroded Spot
- Sinkhole
- Slide or Slip
- Sodic Spot
- Spoil Area
- Stony Spot
- Very Stony Spot
- Wet Spot
- Other

Special Line Features

- Gully
- Short Steep Slope
- Other

Political Features

- Cities

Water Features

- Oceans
- Streams and Canals

Transportation

- Rails
- Interstate Highways
- US Routes
- Major Roads

MAP INFORMATION

Map Scale: 1:18,800 if printed on A size (8.5" × 11") sheet.

The soil surveys that comprise your AOI were mapped at 1:20,000.

Please rely on the bar scale on each map sheet for accurate map measurements.

Source of Map: Natural Resources Conservation Service
Web Soil Survey URL: http://websoilsurvey.nrcs.usda.gov
Coordinate System: UTM Zone 16N NAD83

This product is generated from the USDA-NRCS certified data as of the version date(s) listed below.

Soil Survey Area: Montcalm County, Michigan
Survey Area Data: Version 6, Jun 22, 2009

Date(s) aerial images were photographed: 7/7/2005

The orthophoto or other base map on which the soil lines were compiled and digitized probably differs from the background imagery displayed on these maps. As a result, some minor shifting of map unit boundaries may be evident.

Map Unit Legend

Montcalm County, Michigan (MI117)			
Map Unit Symbol	**Map Unit Name**	**Acres in AOI**	**Percent of AOI**
Ca	Carlisle muck, 0 to 2 percent slopes	9.0	0.6%
Eb	Ensley loam and Edmore loamy fine sand, 0 to 2 percent slopes	5.4	0.3%
Gc	Grayling sand, 0 to 2 percent slopes	6.5	0.4%
Gd	Grayling sand, 2 to 6 percent slopes	37.1	2.3%
Ge	Grayling sand, 6 to 10 percent slopes	29.4	1.8%
Gg	Grayling sand, 10 to 18 percent slopes	22.9	1.4%
Gk	Greenwood and Dawson peats, 0 to 2 percent slopes	2.8	0.2%
Ha	Houghton and Adrian mucks and peats, 0 to 2 percent slopes	0.2	0.0%
Ka	Kawkawlin loam, 0 to 2 percent slopes	0.0	0.0%
Mh	McBride and Isabella sandy loams, 0 to 2 percent slopes	86.5	5.4%
Mk	McBride and Isabella sandy loams, 2 to 6 percent slopes	118.6	7.5%
Mm	McBride and Isabella sandy loams, 6 to 10 percent slopes	110.4	6.9%
Mn	McBride and Isabella sandy loams, 10 to 18 percent slopes	22.6	1.4%
Mt	Montcalm loamy sand and sandy loam, 6 to 10 percent slopes	210.4	13.2%
Mu	Montcalm loamy sand and sandy loam, 10 to 18 percent slopes	74.8	4.7%
Mw	Montcalm and McBride loamy sands and sandy loams, 0 to 2 percent slopes	46.5	2.9%
Mx	Montcalm and McBride loamy sands and sandy loams, 2 to 6 percent slopes	425.3	26.7%
Ra	Rifle and Tawas peats, 0 to 2 percent slopes	81.4	5.1%
W	Water	297.9	18.7%
Wa	Washtenaw loam and silt loam, 0 to 2 percent slopes	0.9	0.1%
Wb	Washtenaw sandy loam and loamy sand, 0 to 2 percent slopes	1.4	0.1%
Totals for Area of Interest		**1,590.1**	**100.0%**

Fish Community and Food Web Responses to a Whole-lake Removal of Coarse Woody Habitat

Greg G. Sass
James F. Kitchell
Stephen R. Carpenter
Thomas R. Hrabik
Anna E. Marburg
Monica G. Turner

Sass is a research associate at the Center for Limnology, University of Wisconsin—Madison and can be reached at ggsass@wisc.edu. Kitchell is the Arthur D. Hasler Professor of Zoology and Director, Center for Limnology, University of Wisconsin—Madison. Carpenter is the Stephen A. Forbes Professor of Zoology at the Center for Limnology, University of Wisconsin—Madison. Hrabik is an associate professor of biology, University of Minnesota—Duluth. Marburg is a graduate student in the Department of Zoology at the University of Wisconsin—Madison. Turner is the Eugene P. Odum Professor of Zoology University of Wisconsin—Madison.

ABSTRACT: As lakeshores are developed, property owners often thin the riparian forest and remove older logs or fallen limbs from the adjacent littoral zone. This practice alters fish habitat and produces unknown ecosystem changes. To assess potential effects on fish communities and food web interactions, we removed more than 75% of the coarse woody habitat (CWH) from the treatment basin of Little Rock Lake, Wisconsin, while leaving the reference basin unaltered. Prior to CWH removal, the food webs in both basins were similar and dominated by aquatic prey. After CWH removal, largemouth bass (*Micropterus salmoides*) in the treatment basin consumed less fish, ate more terrestrial prey, and grew more slowly relative to the population in the reference basin. Yellow perch (*Perca flavescens*) in the treatment basin declined to extremely low densities as a consequence of predation and little or no recruitment. In contrast, perch in the reference basin were replenished by several successful cohorts produced in consecutive years. Maintenance of CWH appears to be crucial for sustaining desirable fishes and fisheries in lakes. Changes in CWH produce complex, long-lasting effects at the ecosystem scale.

GREG SASS

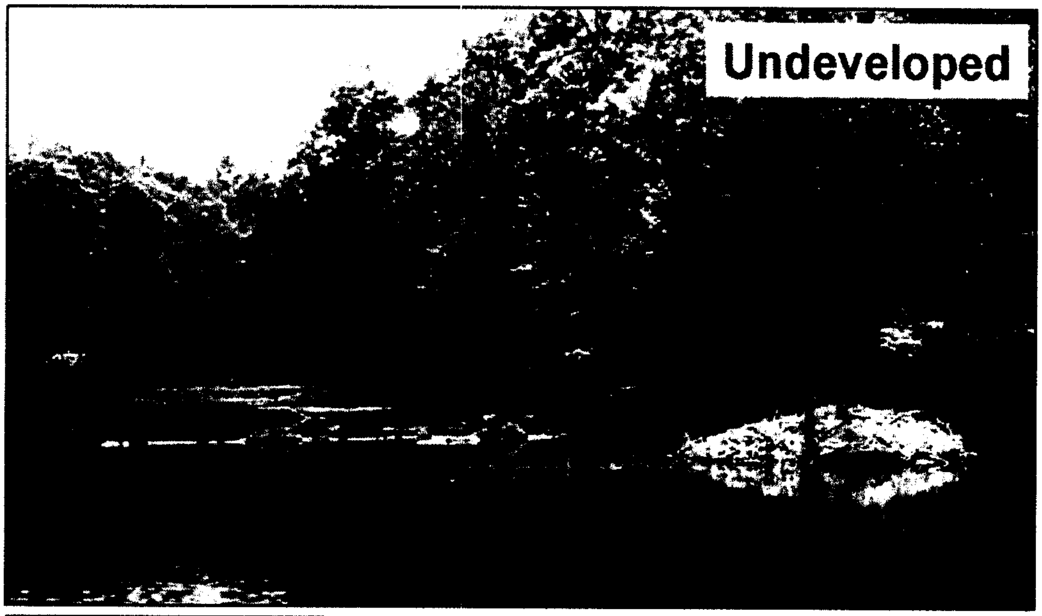
A largemouth bass (*Micropterus salmoides*) swims among submerged CWH in Anderson Lake, Vilas County, WI.

INTRODUCTION

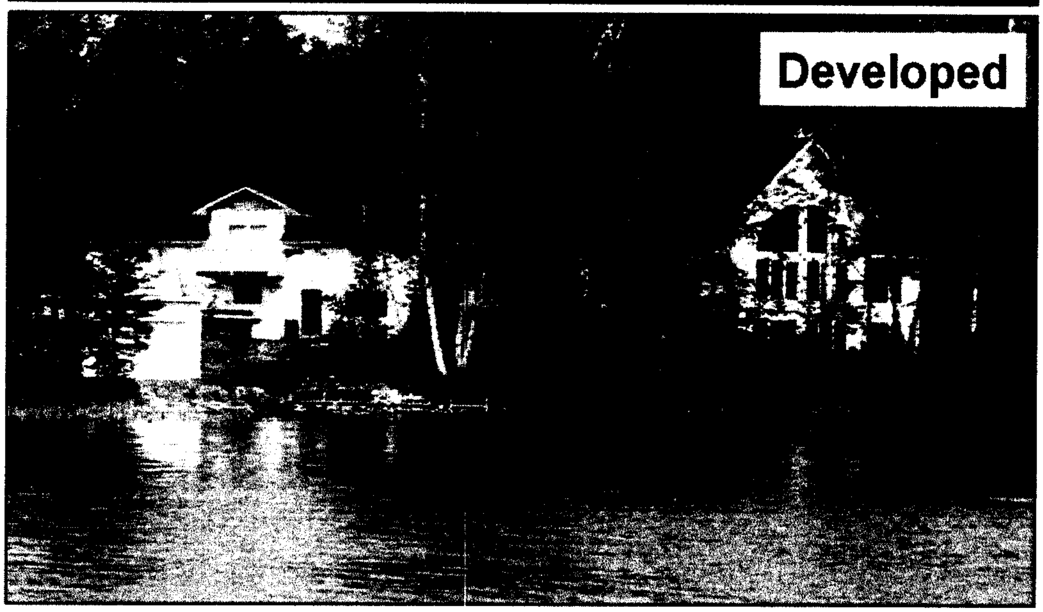
Coarse woody habitat (CWH) may be a critical feature of freshwater ecosystems. In lakes, unlike lotic systems (e.g., Beechie and Sibley 1997; Keim et al. 2002), the role of CWH rarely has been evaluated. CWH supports periphyton, although the direct contribution of epixylic algae to primary productivity in small lakes is relatively minor (Vadeboncoeur and Lodge 2000). The indirect influences of CWH, such as increased organic sediment retention, may be important for epipelic algae, which can provide 50–80% of total production (Hilton et al. 1986; Vadeboncoeur and Lodge 2000). In addition, CWH serves as a substrate for benthic invertebrate production, thereby providing energy to upper trophic levels (Angermeier and Karr 1984; Vander Zanden and Vadeboncoeur 2002).

CWH plays an important role in the life histories of many fish species by offering protection to nesting sites, a spawning substrate, and an area of greater prey availability (Hjelm et al. 2000; Hunt and Annett 2002). CWH may also provide refuge for small fishes because physical structure decreases the foraging success of their predators (Savino and Stein 1982). Savino and Stein (1982) found decreases in largemouth bass (*Micropterus salmoides*) foraging success with increasing levels of simulated aquatic vegetation, and similar constraints could be provided in the interstitial spaces created by CWH. Loss of littoral refuge may result in changes in behavior (Scheuerell and Schindler 2004) and increased mortality rates of juvenile and small fishes, which ultimately depresses growth rates for their predators (Schindler et al. 2000) and increases the potential for depensatory population dynamics (Walters and Kitchell 2001).

Property owners often reduce riparian tree densities and remove CWH from the littoral zones of lakes. A negative relationship existed between CWH abundance and lakeshore residential development in northern Wisconsin and upper Michigan lakes (Christensen et al. 1996; Jennings et al. 2003; Marburg et al. in press; Figure 1). Empirical and model-



GREG SASS



WISCONSIN DEPARTMENT OF NATURAL RESOURCES

Representative photographs compare undeveloped and developed lakeshores typical of northern Wisconsin lakes. The photograph of an undeveloped shoreline was taken from the treatment basin of Little Rock Lake prior to the CWH removal.

STEVE CARPENTER

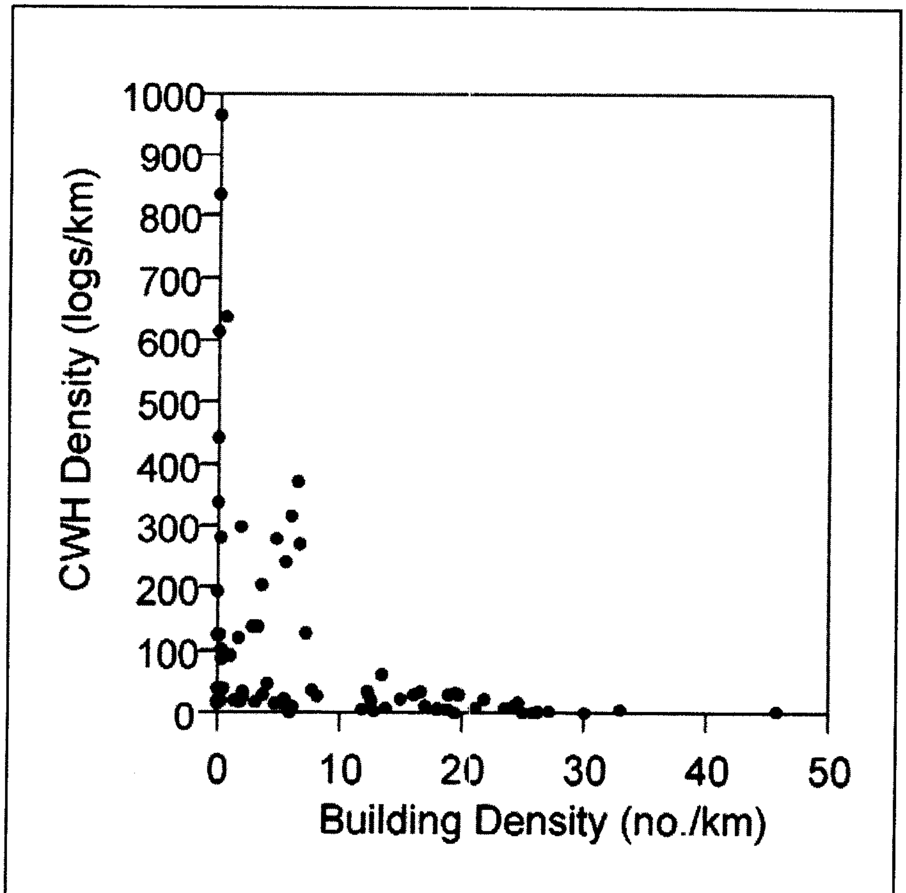
Damon Krueger, Greg Sass, Brian Roth, Jeff Biermann, and Motomi "Genkai" Kato remove coarse woody habitat.

ing studies demonstrate extremely long-lasting negative effects of lakeshore residential development on CWH pools because input rates and decay are slow processes, while human removal rates are fast (Guyette and Cole 1999; Roth unpublished data).

In northern Wisconsin and upper Michigan lakes, growth rates of largemouth bass and bluegill (*Lepomis macrochirus*) were highest in lakes with little or no lakeshore residential development where CWH is most abundant, although trends for bass were not statistically significant (Schindler et al. 2000). This result was surprising because increased nutrient loading due to lakeshore development generally increases lake productivity, and therefore, fish growth rates (Hanson and Leggett 1982). Further, lakeshore development is generally associated with increased angler exploitation, which should reduce density-dependent constraints on growth (Goedde and Coble 1981). The contradiction between expectation and observation suggests that the availability of CWH may create complex relationships between ecosystem productivity, fish growth, and exploitation.

To better understand the role of CWH in aquatic ecosystems, we removed CWH from the littoral zone of the treatment basin of a lake that had no residential development and no fishery. CWH levels in the reference basin of the lake were not manipulated. In this study, we examined the influence of CWH on a coexisting fish predator and prey population. We specifically examined the effects of CWH removal on the aquatic food web and the diet and growth rate of the dominant predator (largemouth bass). We also tested for depensatory population growth dynamics in the dominant prey population, yellow perch (*Perca flavescens*).

Figure 1. The relationship between CWH abundance and the number of buildings per km of shoreline for several northern Wisconsin and upper Michigan lakes. Data from Christensen et al. (1996; CWH >5 cm diameter), Marburg et al. (in press), and previously unpublished data (CWH >10 cm diameter).



MATERIALS AND METHODS

Study Site

Little Rock Lake is an 18 ha, oligotrophic seepage lake located in Vilas County, Wisconsin. The lake has no residential development, has been closed to public access and fishing since 1984, and is divided into two basins by an impermeable curtain which creates a reference (8 ha) and treatment basin (10 ha) for whole-lake studies. The treatment basin was experimentally acidified throughout the late 1980s and then allowed to recover during the 1990s. The aquatic communities were similar in both basins prior to conducting our experiment (Sampson 1999; Hrabik and Watras 2002).

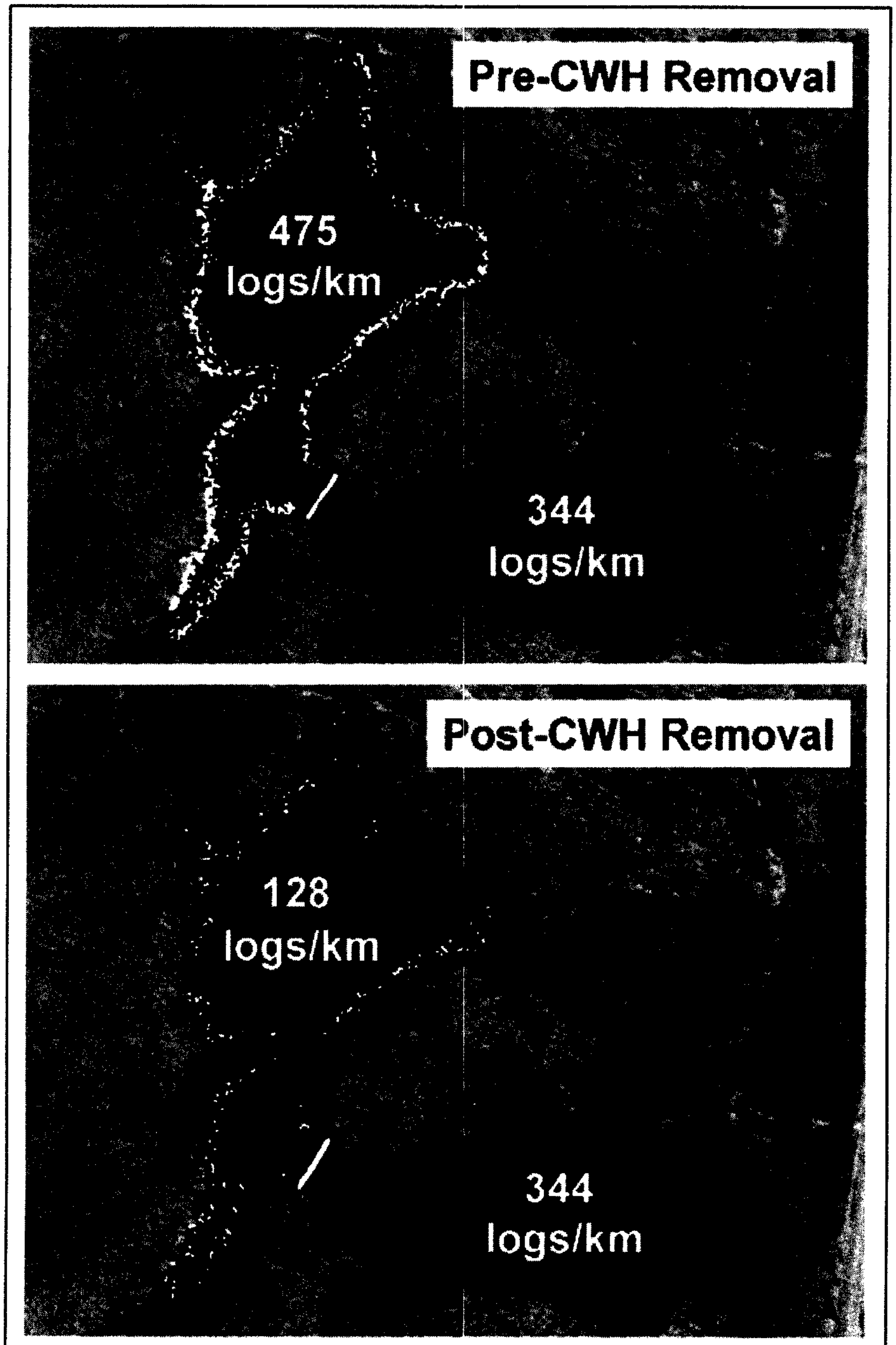
Fish species assemblages in northern Wisconsin lakes are generally dominated by cyprinid-*Umbra* communities where winterkill is prevalent or by centrarchid-esocid-percid communities where winterkill is uncommon and habitat availability and predator-prey interactions determine community structure (Tonn and Magnuson 1982). Little Rock Lake is representative of other northern Wisconsin lakes where winterkill rarely, if ever, occurs. The fish community is dominated by largemouth bass and yellow perch. Less abundant fish species include black crappie (*Pomoxis nigromaculatus*), rock bass (*Ambloplites rupestris*), and central mudminnow (*Umbra limi*). We conducted pre-manipulation monitoring of the fish communities in both basins during July–August 2000, May–September 2001, and May–June of 2002.

Prior to manipulation, the littoral zone in the treatment basin had 475 large logs (>10 cm diameter) per km of shoreline. This level of CWH abundance was above the median for undeveloped lakes in northern Wisconsin and upper Michigan (Christensen et al. 1996; Marburg et al. in press; Figure 2). CWH was the dominant form of littoral structure present. Sparse stands of bur reeds (*Sparganium* spp.) were also present at low stem densities (4.8 stems/m^2). The littoral zone of the reference basin had 344 pieces of large CWH per km of shoreline throughout the study.

During July—August 2002, we removed most of the large CWH from the littoral zone of the treatment basin. Logs and limbs encountered to a depth of 2 m were removed using winches or by hand after reducing the size of the logs with axes or chainsaws. In addition, we removed most small sticks and logs (<10 cm diameter) encountered including three abandoned North American beaver (*Castor canadensis*) lodges and their associated food caches. Removed CWH was placed on shore above the high water mark of the lake.

We reduced large CWH abundance from 475 logs/km of shoreline to 128 logs/km (73% reduction) during the removal (Figure 2). Following CWH removal, the treatment basin had CWH abundances commensurate with lakes having housing densities of 2–8 buildings/km of shoreline, which is representative of a relatively modest level of development for this region (Christensen et al. 1996; Marburg et al. in press; Figure 1). Post-manipulation monitoring of the fish communities was conducted in both basins during August–September 2002 and the May–September periods of 2003 and 2004.

Figure 2.. Aerial photograph of Little Rock Lake with abundances of large (>10 cm diameter) CWH labeled and represented by white dots before and after the CWH removal in the treatment basin (north). The reference basin (south) of Little Rock Lake had 344 logs/km of shoreline throughout the study.



Fish Sampling

Methods employed in this study are detailed in Sass (2004) and briefly recounted here. We collected growth and diet information from the dominant fish species at biweekly intervals during May–September 2001–2004. Largemouth bass, black crappie, and rock bass were collected by hook-and-line angling because the low conductivity of the water precluded effective electroshocking. We collected a total of 963 and 1,209 bass from the reference and treatment basins, respectively, over the 4-year study. Perch were collected with minnow traps and beach seines. Only seined perch were used for diet analysis to prevent bias due to digestion of gut contents from perch captured in minnow traps. We used perch captured in minnow traps and by seine to determine population abundances. We collected a total of 781 and 240 perch from the reference and treatment basins, respectively, from 2001–2004. Each fish captured was measured, weighed, and several scales were taken for age and growth determination. Fishes larger than 150 mm total length were tagged (numbered Floy® tag). We determined diet composition biweekly by performing gastric lavage on up to 15 fish per species. Diet items were separated into major taxonomic categories, enumerated, and dried to determine the dry mass proportion of each prey item in the diet.

Scales were analyzed to determine mean size at age and size-specific growth rates for largemouth bass and perch. Our methods for determining size-specific growth rates and statistical analyses can be found in Schindler et al. (2000). Size-specific growth rates have greater statistical power than other indicators to detect effects of habitat manipulations (Carpenter et al. 1995). Annually, we collected scales from behind the pectoral fin from 5 individual fish of each species for every available 10 mm increment of length (100–109, 110–119 mm, etc.) captured. Bass and perch scales were pressed between glass slides and photographed with a Polaroid DMC 2 digital camera. Scales were read using a Fishomatic optical imaging system developed by the Center for

Limnology at the University of Wisconsin—Madison to determine an individual's growth rate in the previous year. Growth was determined by the Fraser-Lee method of back-calculating the length of the previous year. We then regressed $\log_e$ growth rate (mm/y; dependent variable) on fish size (mm; independent variable) for each species in each year of the study to determine mean growth rates for four common size classes of bass (100, 200, 300, 400 mm total length) and perch (50, 100, 150, 200 mm total length; Carlander 1982; Schindler et al. 2000). Only one size-specific growth rate was calculated from each individual fish. A total of 318 bass (pre-CWH removal = 132, post- = 186) and 93 perch (pre- = 68, post- = 25) were analyzed for growth from the reference basin in 2001–2004. We analyzed 320 bass (pre-CWH removal = 134, post- = 186) and 96 perch (pre- = 57, post- = 39) from the treatment basin over the same time period.

We used a Chapman-modified, continuous Schnabel mark-recapture population estimation procedure to estimate adult bass and total perch abundances in each year of the study (Ricker 1975). We did not estimate young-of-year (YOY) bass abundances. To determine young-of-year (YOY) and total perch catch per unit of effort (CPUE), we deployed 10 minnow traps in 2003 and 20 traps in 2004 biweekly in each basin at pre-specified near-shore locations from May–September. Perch YOY typically became vulnerable to minnow trapping during July and were less than 75 mm in length. Each trap was deployed for five days and catches were counted and emptied at one or two day intervals.

Analysis

We used a Model I single factor Analysis of Variance (ANOVA) within basins (Zar 1996) and paired t-tests among basins to test for differences in the proportion of terrestrial prey items and average weight per bass diet before and after the CWH removal. To test for statistically significant differences in size-specific bass growth rates, we examined 95% confidence intervals from the regression line relationships between growth rate and fish size in each basin. All least squares regressions for the relationship between $\log_e$ growth rate (mm/y) versus fish size for each species were statistically significant (P <0.001) and had r^2 values ranging from

Figure 3. Proportion of largemouth bass (Micropterus salmoides) diets (A) consisting of yellow perch (*Perca flavescens*) and density (B) of yellow perch in the reference (R) and treatment (T) basins of Little Rock Lake prior to (pre-) and following (post-) the CWH removal.

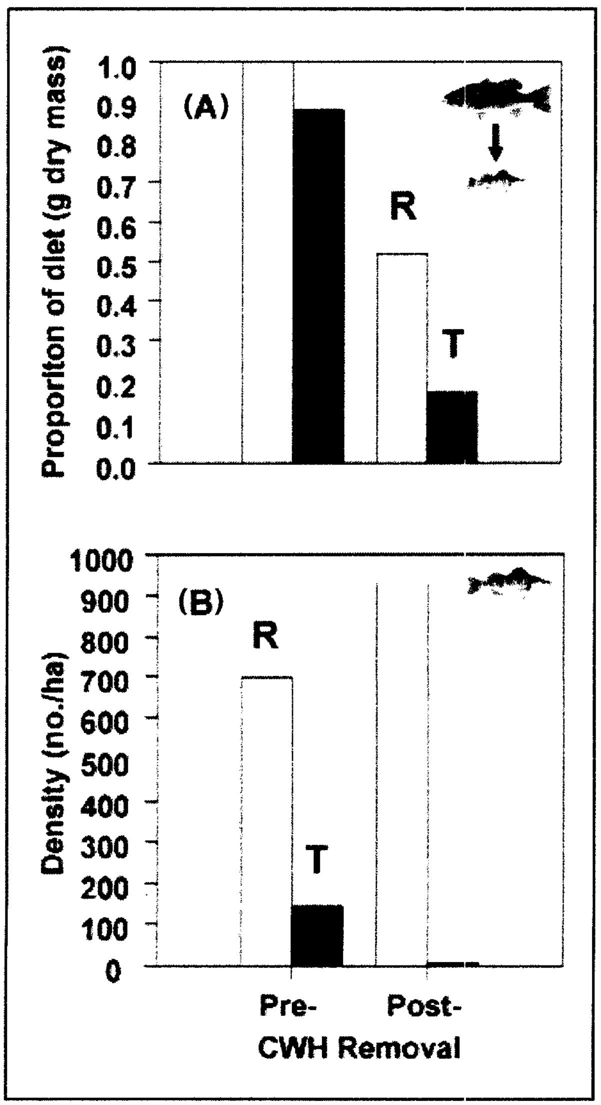
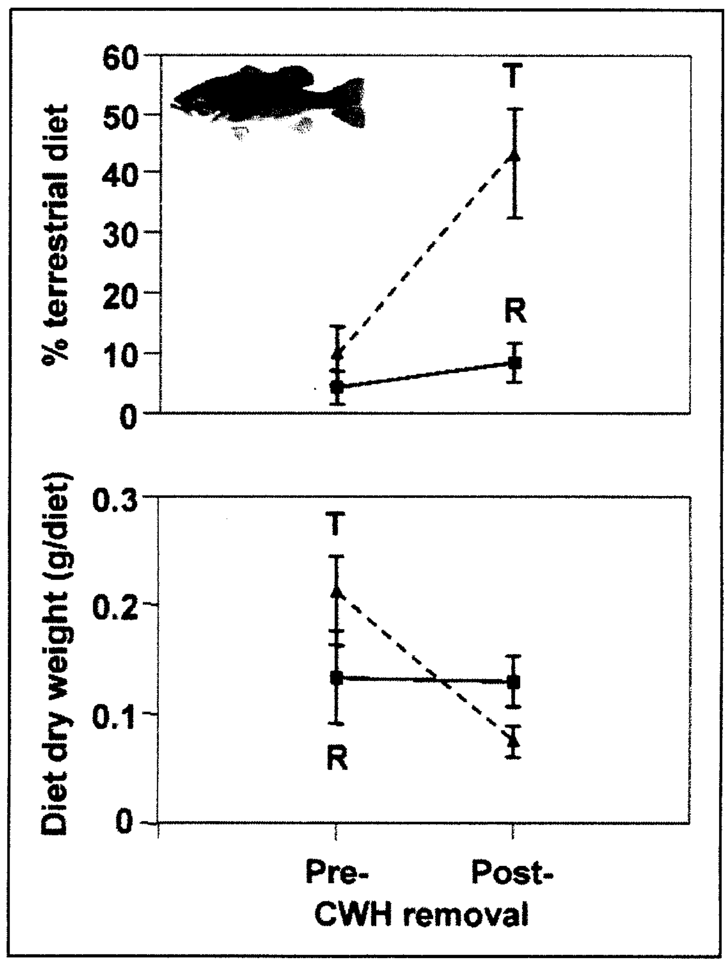


Figure 4. Trends in the proportion of terrestrial prey and the average dry weight per diet for largemouth bass (*Micropterus salmoides*) in the reference (R, ■, solid line) and treatment (T, ▲, dashed line) basins of Little Rock Lake prior to (pre-) and following (post-) the CWH removal. Error bars represent the standard error about the mean.



0.33 to 0.63. Overlap of 95% confidence intervals for a particular size-specific growth rate (i.e., x = 100, 200, 300, 400 mm for largemouth bass) between basins represented no significant difference in growth rates. Statistical differences in all metrics were assessed at the $P = 0.05$ level with a null hypothesis of no difference between means.

RESULTS

Food Web Responses

Pre-CWH Removal (Both Basins)

The food webs of both basins were dominated by aquatic prey prior to the CWH removal. Prior to manipulation, bass primarily consumed perch and perch consumed benthic invertebrates. Yellow perch averaged 93% and 81% of the total diet of bass in the reference and treatment basins, respectively (Figure 3A). Perch diets did not change during the study and were dominated by consumption of trichopterans, dipterans, and odonate larvae. Black crappie and rock bass diets were comprised of dipteran larvae (*Chaoborus* spp.) and benthic invertebrates (Odonata, Trichoptera), respectively, throughout the study.

The terrestrial component of bass diets (paired t-test; $n = 10$; df = 9; $t = 1.3$; $P = 0.22$) and total weight per diet (paired t-test; $n = 10$; df = 9; $t = 0.34$; $P = 0.74$) did not differ between basins prior to the CWH removal (Figure 4). Terrestrial vertebrates and invertebrates made up 5% to 9% of bass diets by dry weight in the reference basin and 9% to 12% in the treatment basin prior to the CWH removal.

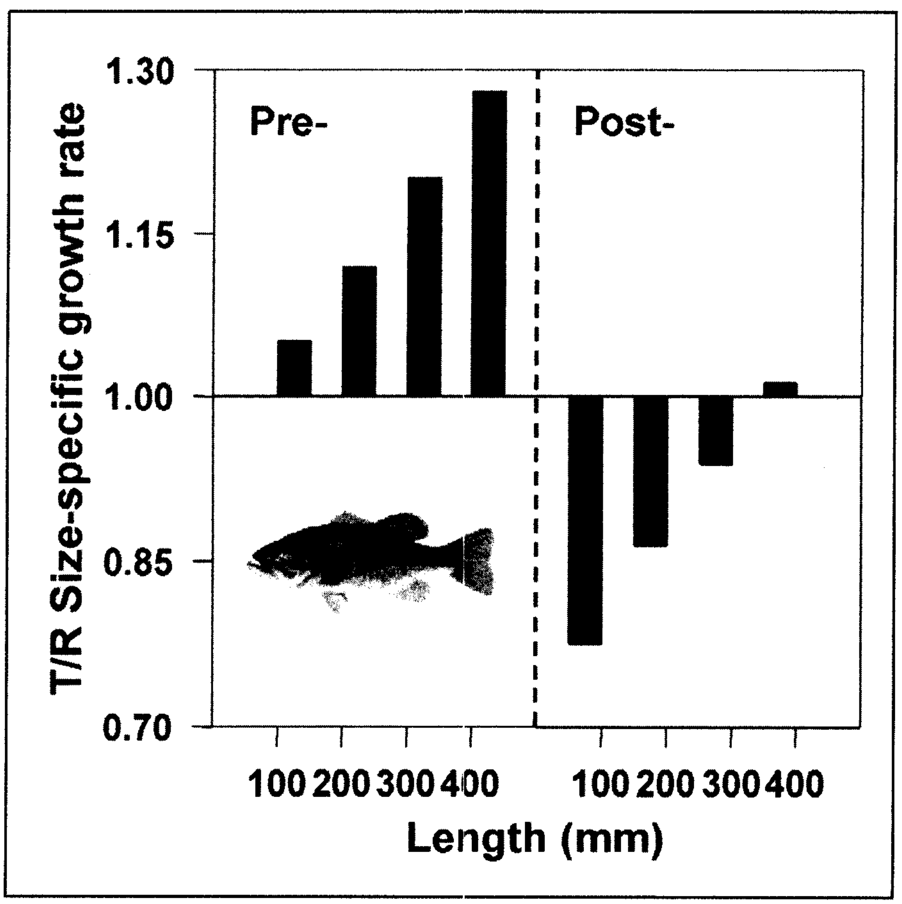
Post-CWH Removal (Reference Basin)

Little change was observed in the food web of the reference basin following the CWH removal. Perch consumption decreased from 93% to 62% of the total bass diet by dry mass, but increased in 2004 after an initial decrease (Figure 3A). No significant change was observed in the proportion of terrestrial prey found in bass diets (ANOVA; $n = 25$; df = 1,23; $F = 2.3$; $P = 0.14$) or in consumption rates (ANOVA; $n = 25$; df = 1,23; $F = 0.62$; $P = 0.44$) in the reference basin throughout the study (Figure 4). Terrestrial prey comprised 17% to 19% of bass diets in the reference basin following the manipulation of the treatment basin.

Post-CWH Removal (Treatment Basin)

The treatment basin food web switched from one dominated by aquatic prey to one increasingly subsidized by terrestrial prey following CWH removal. After the CWH removal, perch averaged only 14% of the diet of bass in the treatment basin (Figure 3A). The terrestrial component of bass diets increased significantly within the treatment basin (ANOVA; $n = 26$; df = 1,25; $F = 8.6$, $P = 0.007$) and between basins (paired t-test; $n = 15$; df = 14; $t = 4.5$, $P < 0.001$) following the CWH removal (Figure 4). In addition, we observed a significant decrease in consumption rate by bass within the treatment basin (ANOVA; $n = 26$; df = 1,25; $F = 10.7$; $P = 0.003$) and when compared to the reference basin (paired t-test; $n = 15$; df = 14; $t = 2.5$; $P = 0.02$; Figure 4). Terrestrial vertebrates and invertebrates comprised 51% to 55% of treatment basin bass diets by dry mass following the CWH removal.

Figure 5. Ratio of treatment basin (T) largemouth bass (*Micropterus salmoides*) size-specific growth rate to reference basin (R) size-specific growth rate for 100, 200, 300, and 400 mm size classes in Little Rock Lake before (pre-) and after (post-) the CWH removal.



Growth Responses

Growth rates of bass in the treatment basin decreased relative to those observed in the reference basin following the CWH removal. Prior to manipulation, mean size-at-age and size-specific growth rates at four lengths were significantly higher for bass in the treatment basin (Sass 2004; Figure 5). After manipulation, mean size at age and size-specific growth rates declined and were most notable for younger age and smaller size classes of bass in the treatment basin (Sass 2004; Figure 4). No change in perch growth occurred during the study period.

Fish Community Responses

The perch population of the treatment basin declined rapidly following the CWH removal and remained at low abundances. In contrast, the density of perch in the reference basin increased during the study period (Figure 3B). Average density of the population in the reference basin was 815 perch/ha during the study. Estimated population density in the treatment basin was 141 perch/ha prior to CWH removal.

Population estimates for perch could not be calculated in the treatment basin after the CWH removal because no marked perch were recaptured. Based on catch rate data, current densities of perch have been as low as five perch/ha in the treatment basin. Adult bass densities were higher within and among basins during the study ranging from 56 (95% confidence interval; 41, 86) to 112 (85, 159) bass/ha in the reference basin and from 60 (44, 82) to 82 (63, 113) bass/ha in the treatment basin, but the increases were not statistically significant ($P > 0.05$). Black crappie and rock bass densities remained low and unchanged throughout the study.

Young-of-year perch recruitment was minimal in the treatment basin following the CWH removal. The total catch of YOY perch (n = 20 YOY perch/10 ha) following the CWH removal in the treatment basin indicated a potential density of 2 YOY/ha. The density of YOY perch in the reference basin was up to 16 times greater (n = 256 YOY perch/8 ha) during the same period.

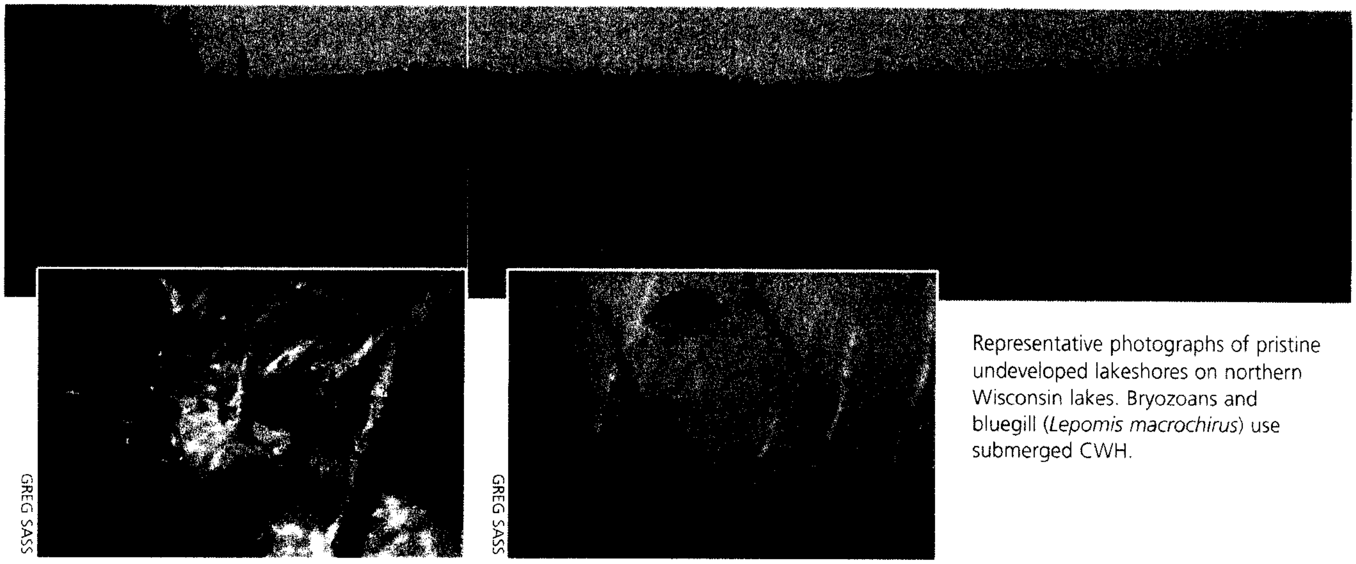
DISCUSSION

Changes in the diets of treatment basin bass following the CWH removal were caused by rapid reductions in perch abundance due to intensified bass predation, and perhaps from loss of woody substrate for benthic invertebrate production (Angermeier and Karr 1984). The slight reduction in perch consumption by reference basin bass following the CWH removal likely represents a cyclic, stable predator-prey dynamic between bass and perch (Hinke 2001). Perch populations are generally dominated by a strong cohort that is reduced in number over time by predation until a compensatory stock-recruitment response occurs and another strong year class is produced. Declines in perch consumption by reference basin bass immediately following the CWH removal likely represent the predator-induced perch decline and their decreased overall availability. In contrast to the treatment basin, perch consumption by reference basin bass has increased toward pre-manipulation levels coincident with several strong, consecutive year classes of perch and their subsequent increased availability.

Although both basins have similar morphometry and therefore, similar availability of terrestrial prey, the food web of the treatment basin was largely subsidized by terrestrial sources of food after CWH removal. For example, about 50% of treatment basin bass diets by dry weight were terrestrial vertebrates and invertebrates following the removal as compared to about 10% prior to manipulation. The diets of bass in the treatment basin reflected optimal foraging tenets following the removal of CWH (Werner and Hall 1974). Hodgson and Kitchell (1987) report a similar result where bass in two lakes maintained high diet breadth when intra-specific competition was high, and then switched to more profitable prey items (e.g., fishes, odonate nymphs) and reduced diet breadth when competition was relaxed following a 50% reduction in bass density. Removal of CWH from the treatment basin and the associated decline in perch abundance coincided with bass reliance upon terrestrial prey (e.g., frogs, snakes, rodents, insects), benthic invertebrates, and less abundant and smaller prey fishes such as YOY bass, YOY perch, and central mudminnow. The change in diet to less abundant and less energetically favorable prey foreshadowed the observed declines in largemouth bass growth rates and was consistent with trends reported by Schindler et al. (2000). Cannibalism in this study was observed only from bass in the treatment basin following CWH removal. Similarly, bass cannibalism contributed to a major proportion of the diet in upper Michigan lakes with no lakeshore residential development, high densities of bass with poor growth rates, and low alternative prey fish availability (Schindler et al. 1997).

Depressed growth rates and increased incidence of cannibalism may result in stunting of a bass population (Schindler et al. 1997; Post et al. 1998; Post 2003) and also creates the potential for the perch population to recover if cyclic predator-prey interactions occur as a consequence of compromised bass recruitment (Hinke 2001). Our study suggests a low probability of perch recovery because adult bass densities increased throughout the study (proxy for sufficient bass recruitment), the incidence of cannibalism observed was low, and cyclic predator-prey dynamics are often habitat-mediated (Hinke 2001). More likely, perch population biomass declines from bass predation and subsequent energy transfer to the bass population in the treatment basin have resulted in improved bass recruitment, as suggested by the increase in adult bass densities. Mass-balance food web modeling exercises simulating the Little Rock Lake manipulation suggest extirpation of the perch population and increased bass population biomasses following CWH removal (Roth unpublished data). Mechanistically, bass biomass replaces perch biomass in order to return the system to its carrying capacity (Roth unpublished data). Similar ecosystem-scale mass-balance modeling approaches, such as Ecopath with EcoSim, show compensatory biomass increases in predators or prey when one biomass pool declines and pools are linked by food web interactions (Walters et al. 2000; Hinke et al. 2004).

Patterns observed in bass diet composition, perch population estimates, and YOY perch catch rates in the treatment basin evidence a rapid and persistent decline in the perch population following the CWH removal. Although perch abundance in each basin was variable and both were declining, but persistent, prior to the CWH removal (Swenson 2002; Sass 2004), the reference system demonstrated an opposite response through compensatory recruitment and the production of several cohorts of perch. Perch use CWH as a spawning substrate, foraging site, and as a refuge from predators. Therefore, the removal of CWH imposed an increase in predation mortality, a decrease in prey availability, and a loss of spawning habitat. This combination may have decreased the reproductive potential of the treatment basin population to levels at or below the replacement rate due to the additive effects of depensatory mechanisms and could cause the population to collapse (Post et al. 2002; Carpenter 2003). The treatment basin population may have an extremely low probability of recovery and could be vulnerable to extirpation as a consequence of: (1) low abundance of spawning substrate, (2) few or no adult spawners, (3) continued predation pressure by bass on the few remaining adult perch, (4) intense predation by bass on any YOY perch produced, and (5) extremely slow input rates of natural CWH. Much the same set of constraints would be imagined for other prey fish species and, over time, might produce a less diverse fish community. Opening the lake to fishery exploitation might reverse that trend, but the interactions of habitat change and exploitation effects have not been evaluated experimentally.



Representative photographs of pristine undeveloped lakeshores on northern Wisconsin lakes. Bryozoans and bluegill (*Lepomis macrochirus*) use submerged CWH.

Our study suggests that CWH may play a similar, but also potentially different, role as aquatic macrophytes and other forms of structure (e.g., rocky shorelines) in lakes. High densities of simulated and natural aquatic macrophytes decrease the foraging success of predators (Savino and Stein 1982; Gotceitas and Colgan 1989, 1990). The interstitial spaces and structural complexity provided by high abundances of littoral CWH likely play a similar role in decreasing foraging success of predators, as evidenced by the rapid decline of the perch population following the CWH removal in this study. In contrast to our study, cutting channels through dense beds of the invasive macrophyte Eurasian water milfoil (*Myriophyllum spicatum*) has elevated growth rates of largemouth bass and bluegill (Olson et al. 1998). In this case, cutting channels increased habitat by increasing the length of the weedline. While low levels of CWH (Schindler et al. 2000; Sass 2004) and high densities of aquatic macrophytes (Olson et al. 1998) may result in depressed fish growth rates, intermediate levels of structure may provide the highest fish growth rates because predators are able to forage sufficiently, but are not capable of annihilating prey populations (Crowder and Cooper 1982). Because CWH cannot provide the impenetrable cover of certain macrophyte species (e.g., Eurasian water milfoil), CWH loss may have greater impacts on fish populations than macrophyte loss (Schindler et al. 2000; Sass 2004).

While some lakes in northern Wisconsin are known for high floristic quality, aquatic macrophyte abundances are also being compromised by lakeshore residential development pressures in a similar fashion as CWH (Radomski and Goeman 2001; Jennings et al. 2003). Establishment of exotic rusty crayfish (*Orconectes rusticus*) in many northern Wisconsin lakes and their negative impacts on aquatic macrophyte abundances also reduce available structure for fishes (Wilson 2002). However, in contrast to the high regenerative capabilities of aquatic macrophytes (Olson et al. 1998; Wilson 2002), natural replacement and degradation rates of CWH in northern lakes are very slow (Guyette and Cole 1999). Thus, CWH loss may have greater and longer-term effects on fish populations. Solely, or in concert, CWH and aquatic macrophyte removals may result in fish species diversity losses and depressed fish growth rates. Indeed, Tonn and Magnuson (1982) found that predator-prey interactions and structural habitats were critical variables in determining fish community structure in a number of northern Wisconsin lakes.

MANAGEMENT IMPLICATIONS

The manipulation of Little Rock Lake changed CWH abundances from numbers commensurate with other undeveloped lakes in northern Wisconsin to those with modest or intermediate lakeshore housing densities (Christensen et al. 1996; Marburg et al. in press; Figure 1). More buildings and people generally correspond with increased fishery exploitation (NRC 1992), lower fish population densities (Swenson 2002), and greater fish growth rates in response to reduced competition (Goedde and Coble 1981). Instead, we speculate that fishery exploitation interacts with removal of CWH to create a change in ecosystem state where fish populations exhibit the paradox of both lower population densities and reduced individ-

Brian Roth removes CWH from the treatment basin of Little Rock Lake.

MICHAEL MEYER

MICHAEL MEYER

MICHAEL MEYER

ual growth rates (Roth unpublished data). Although such patterns have been observed for bluegill populations (Ehlinger 1997; Schindler et al. 2000), in general, our results suggest that fish production had substantially declined.

In small, oligotrophic lakes such as those in northern Wisconsin, benthic primary production and exogenous sources of carbon fuel aquatic food webs (Vadeboncoeur and Lodge 2000; Pace et al. 2004). Our experimental removal of CWH shows that this aspect of human development has rapid and strong effects on the food webs and fish communities of lakes. Removal of CWH may result in decreased benthic invertebrate production, a reduction or collapse of prey populations that depend on CWH for refuge and spawning substrate, and depressed fish growth rates and production. The inverse correlation of lakeshore development and fish growth (Schindler et al. 2000) may be best explained by strong bottom-up effects of decreasing primary and secondary productivity and strong top-down effects by predators depleting prey fish resources when CWH is removed. While winterkill events and predation are key factors structuring fish communities, adequate refuge may depress predator foraging success and mediate the coexistence of predator and prey populations in lakes (Tonn and Magnuson 1982).

CWH can be removed from lakes and shorelines in a few months or years as shoreline development gradually proceeds, but natural replacement takes centuries (Guyette and Cole 1999). As development proceeds, CWH declines over time and predator populations may decline to abundances that can be supported by the reduced prey populations. Thus, CWH removal may have extremely long lasting or even permanent consequences for fish populations, fisheries, and the food webs that support them.

Management policies can respond to this reality. Limitations can be placed on the extent of shoreline development and/or the amount of trees or CWH removed from the riparian and littoral zones of the lake, respectively. Alternatively, undeveloped shoreline can be promoted as an ecological reserve essential to the maintenance of desirable food webs that support important recreational fisheries and/or CWH can be added back to create littoral habitat. An ongoing whole-lake study, which added trees to the littoral zone of a lake with low amounts of CWH to determine if CWH loss was reversible, will shed light on the latter as a viable management option (Sass unpublished data). Clearly, there are strong trade-offs between landscaped lawns with clean sand beaches and the natural littoral zone habitats that support desirable fisheries. In both cases, education and outreach are essential as we learn more about the ecological benefits of leaving logs in the lakes.

ACKNOWLEDGEMENTS

We thank Jeff Biermann, Andrea Fowler, Jon Hansen, Adam Kautza, Michelle Nault, Steve Reinhardt, Scott Van Egeren, J. J. Weis, and Michele Woodford for field assistance. We are indebted to all (n ~30) who helped with the CWH removal and in particular, appreciate the hard work of Matt Helmus, Motomi "Genkai" Kato, Damon Krueger, Brad Ray, and Brian Roth. We owe special thanks to the Wisconsin Department of Natural Resources for approving this project and are particularly grateful to Jeff Bode, Steve Gilbert, and Jayne Wade for their support. This research was funded by a National Science Foundation Integrated Graduate Education and Research Traineeship (IGERT) awarded to G. G. Sass and an NSF biocomplexity grant (DEB-0083545) awarded to S.R. Carpenter. Equipment was provided by the Anna Grant Birge Memorial fund to G. G. Sass.

REFERENCES

Angermeier, P. L., and **J. R. Karr.** 1984. Relationship between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113:716-726.

Beechie, T. J., and **T. H. Sibley.** 1997. Relationships between channel characteristics, wood debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126:217-229.

Carlander, K. D. 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. Transactions of the American Fisheries Society 111:332-336.

Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. International Ecology Institute, Oldendorf/Luhe, Germany.

Carpenter, S. R., P. Cunningham, S. Gafny, A. Munoz del Rio, N. Nibbelink, M. Olson, T. Pellet, C. Storlie, and **A. Trebitz.** 1995. Responses of bluegill to habitat manipulations: power to detect effects. North American Journal of Fisheries Management 15:519-527.

Christensen, D. L., B. R. Herwig, D. E. Schindler, and **S. R. Carpenter.** 1996. Impacts of lakeshore development on coarse woody debris in north temperate lakes. Ecological Applications 6:1143-1149.

Crowder, L. B., and **W. E. Cooper.** 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813.

Ehlinger, T. J. 1997. Male reproductive competition and sex-specific growth patterns in bluegill. North American Journal of Fisheries Management 17:508-515.

Goedde, L. E., and **D. W. Coble.** 1981. Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin lakes. Transactions of the American Fisheries Society 110:594-603.

Gotceitas, V., and **P. Colgan.** 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80:158-166.

______. 1990. The effects of prey availability and predation risk on habitat selection by juvenile bluegill sunfish. Copeia 1990:409-417.

Guyette, R. P., and **W. G. Cole.** 1999. Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone. Canadian Journal of Fisheries and Aquatic Sciences 56:496-505.

Hanson, J. M., and **W. C. Leggett.** 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39:257-263.

Hilton, J., J. P. Lishman, and **P. V. Allen.** 1986. The dominant mechanisms of sediment distribution and focusing in a small, eutrophic, monomictic lake. Limnology and Oceanography 31:125-133.

Hinke, J. T. 2001. Trophic interactions of juvenile yellow perch (*Perca flavescens*) and young-of-year largemouth bass (*Micropterus salmoides*): the influences of density, size, and growth. Master's thesis, University of Wisconsin—Madison.

Hinke, J. T., I. C. Kaplan, K. Aydin, G. M. Watters, R. J. Olson, and **J. F. Kitchell.** 2004. Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. Ecology and Society 9(1).

Hjelm, J., L. Persson, and **B. Christensen.** 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122:190-199.

Hodgson, J. R., and **J. F. Kitchell.** 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). American Midland Naturalist 118:323-336.

Hrabik, T. R., and **C. J. Watras.** 2002. Recent declines in mercury concentration in a freshwater fishery: isolating the effects of de-acidification and decreased atmospheric mercury deposition in Little Rock Lake. Science of the Total Environment 297:229-237.

Hunt, J., and **C. A. Annett.** 2002. Effects of habitat manipulation on reproductive success of individual largemouth bass in an Ozark reservoir. North American Journal of Fisheries Management 22:1201-1208.

Jennings, M. J., E. E. Emmons, G. R. Hatzenbeler, C. Edwards, and **M. A. Bozek.** 2003. Is littoral habitat affected by residential development and land use in watersheds of Wisconsin lakes? Lake and Reservoir Management 19:272-279.

Keim, R. F., A. E. Skaugset, and **D. S. Bateman.** 2002. Physical aquatic habitat II. Pools and cover affected by large woody debris in three western Oregon streams. North American Journal of Fisheries Management 22:151-164.

Marburg, A. E., M. G. Turner, and **T. K. Kratz.** 2006. Natural and anthropogenic variation in coarse wood among and within lakes. Journal of Ecology: in press.

National Research Council. 1992. Restoration of aquatic ecosystems. National Academy Press, Washington, DC.

Olson, M. H., S. R. Carpenter, P. Cunningham, S. Gafny, B. R. Herwig, N. P. Nibbelink, T. Pellett, C. Storlie, A. S. Trebitz, and **K. A. Wilson.** 1998. Managing aquatic macrophytes to improve fish growth: a multi-lake experiment. Fisheries 23(2):6-12.

Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, J. R. Hodgson, M. C. Van de Bogert, D. L. Bade, E. S. Kritzberg, and **D. Bastviken.** 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427:240-243.

Post, D. M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology 84:1298-1310.

Post, D. M., J. F. Kitchell, and **J. R. Hodgson.** 1998. Interactions among adult demography, spawning date, growth rate, predation, overwintering mortality, and the recruitment of largemouth bass in a northern lake. Canadian Journal of Fisheries and Aquatic Sciences 55:2588-2600.

Post, J. R., M. Sullivan, S. P. Cox, N. P. Lester, C. J. Walters, F. A. Parkinson, A. J. Paul, L. Jackson, and **B. J. Shuter.** 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27(1):6-17.

Radomski, P., and **T. Geoman.** 2001. Consequences of human lakeshore development on emergent and floating-leaf vegetation abundance. North American Journal of Fisheries Management 21:46-61.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Sampson, C. J. 1999. Aquatic chemistry of Little Rock Lake, Wisconsin, duringacidification and recovery. Ph.D thesis, University of Minnesota—Twin Cities.

Sass, G. G. 2004. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Ph.D. thesis, University of Wisconsin—Madison.

Savino, J. F., and **R. A. Stein.** 1982. Predator-prey interaction between largemouth bass and bluegills as influence by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255-266.

Scheuerell, M. D., and **D. E. Schindler.** 2004. Changes in the spatial distribution of fishes in lakes along a residential development gradient. Ecosystems 7:98-106.

Schindler, D. E., J. R. Hodgson, and **J. F. Kitchell.** 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia 110:592-600.

Schindler, D. E., S. I. Geib, and **M. R. Williams.** 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems 3:229-237.

Swenson, W. A. 2002. Demographic changes in a largemouth bass population following closure of the fishery. Pages 627-637 *in* D. P. Philipp and M. S. Ridgway, eds. Black bass: ecology, conservation, and management. American Fisheries Society, Bethesda, Maryland.

Tonn, W. M., and **J. J. Magnuson.** 1982. Patterns in species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149-1166.

Vadeboncoeur, Y., and **D. M. Lodge.** 2000. Periphyton production on wood and sediment: substratum-specific response to laboratory and whole-lake nutrient manipulations. Journal of the North American Benthological Society 19:68-81.

Vander Zanden, M. J., and **Y. Vadeboncoeur.** 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152-2161.

Walters, C. J., D. Pauly, V. Christensen, and **J. F. Kitchell.** 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3:70-83.

Walters, C. J., and **J. F. Kitchell.** 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences 58:39-50.

Werner, E. E., and **D. J. Hall.** 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

Wilson, K. A. 2002. Impacts of the invasive rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. Ph.D. thesis, University of Wisconsin—Madison.

Zar, J. H. 1996. Biostatistical analysis, third edition. Prentice Hall, New Jersey.