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

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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.

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 rela-

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

tionship 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-
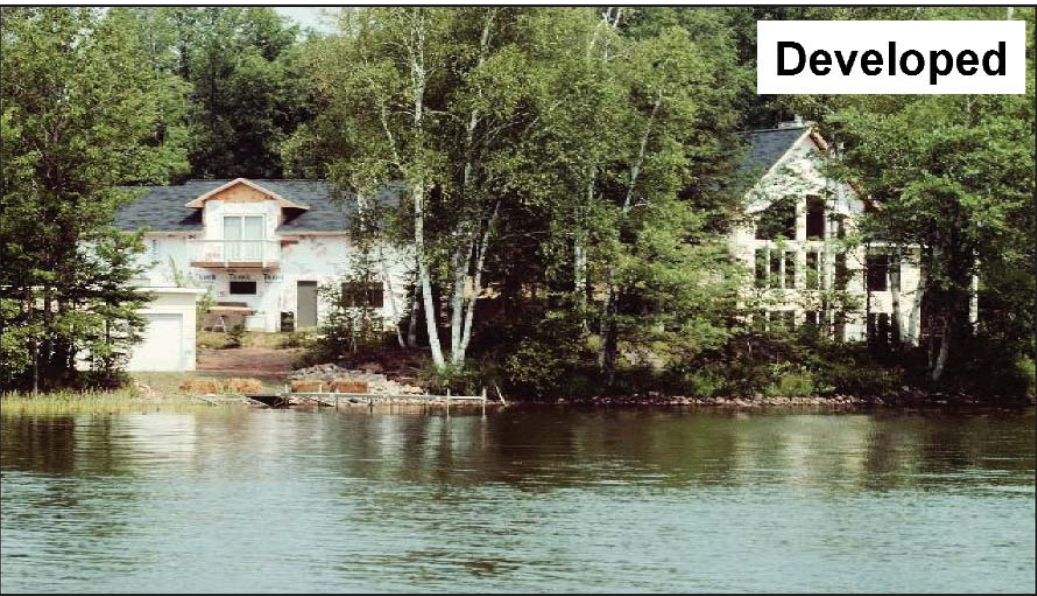
Undeveloped

GREG SASS

Developed

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.

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).
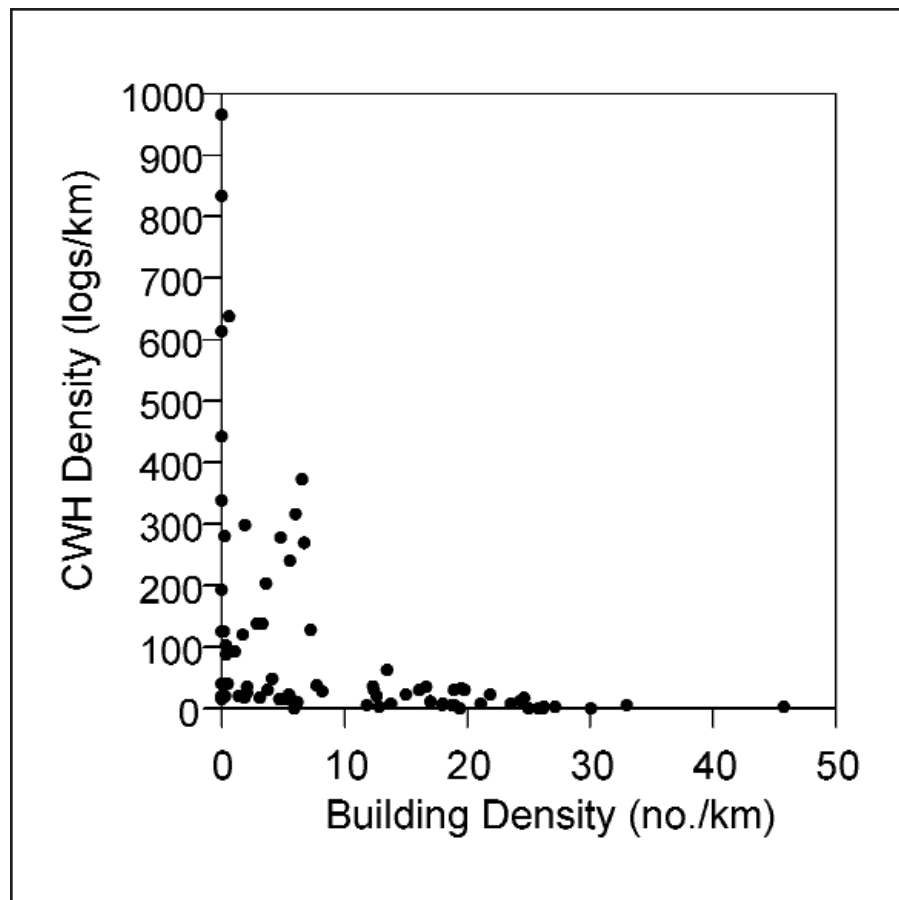

MATERIALS AND METHODS

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 repre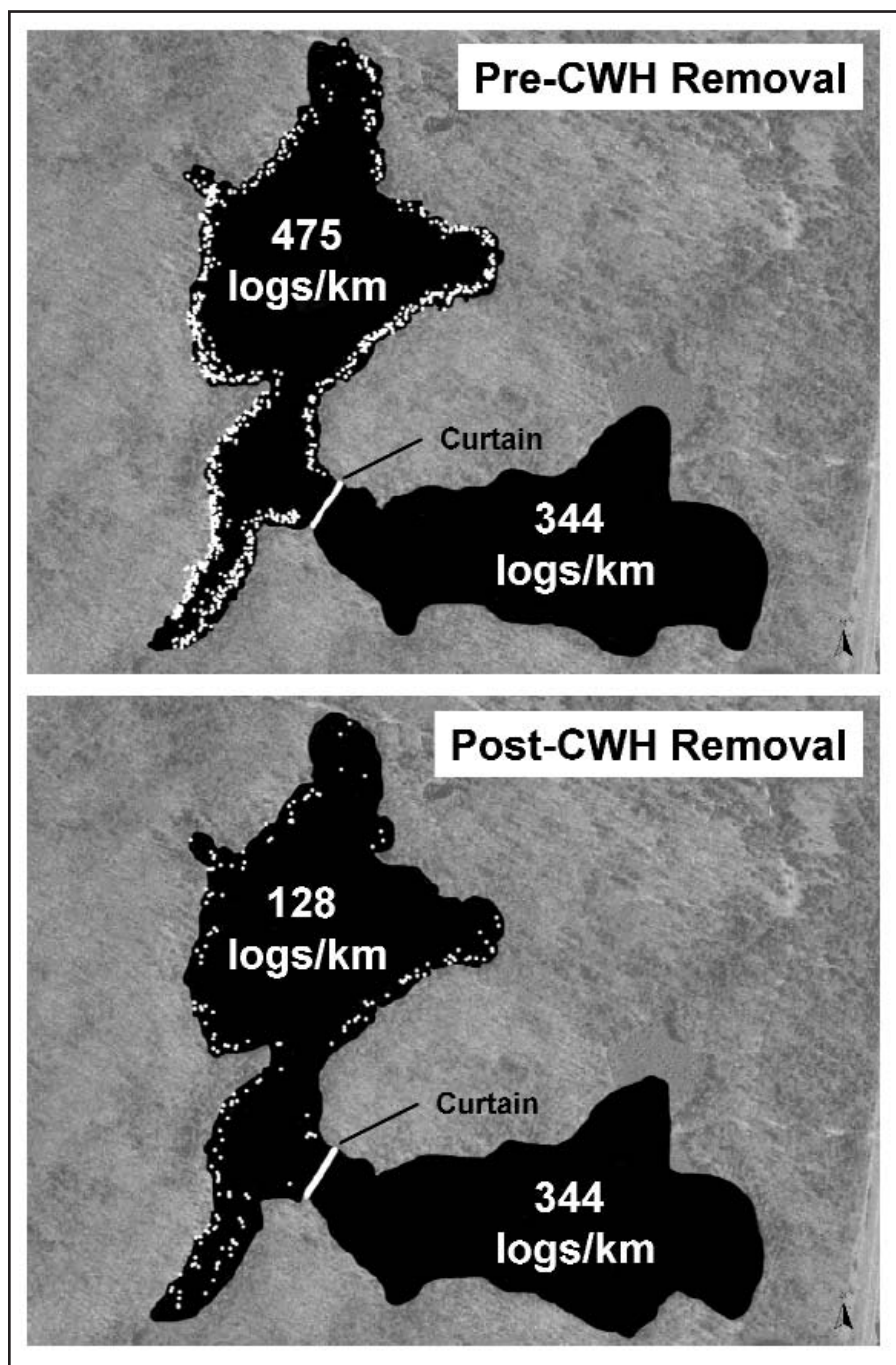sentative of a relatively modest level of development for this region (Christensen et al. 1996; Marburg et al. in press; Figure 1). Post-manipulation monitoring of the fish communities was conducted in both basins during August–September 2002 and the May–September periods of 2003 and 2004.

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

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.

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.
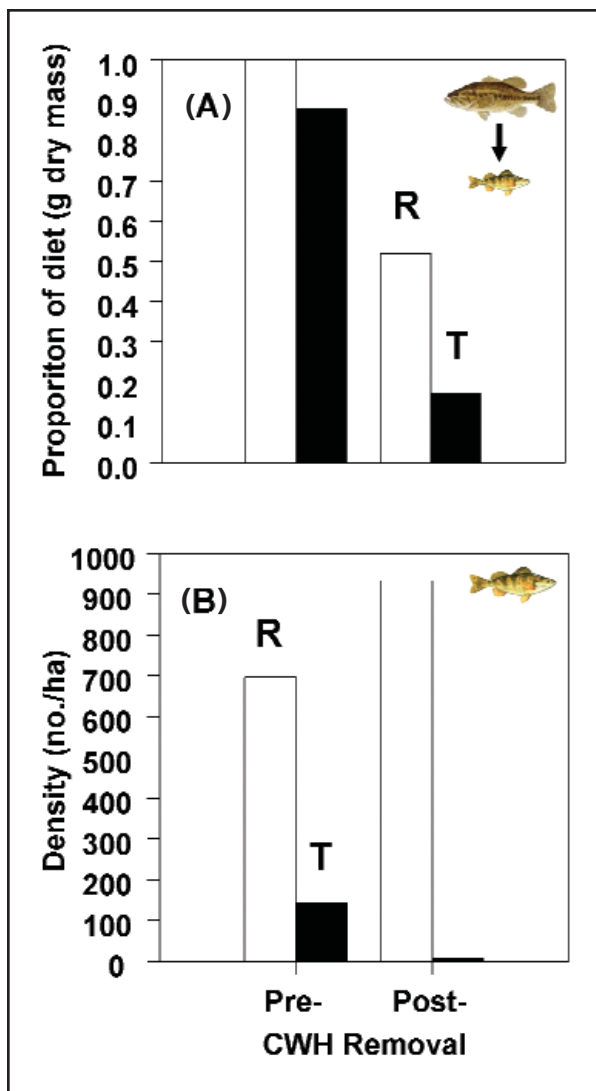
We used a Chapman-modified, continuous Schnabel mark-recapture population estimation procedure to estimate adult bass and total perch abundances in each year of the study (Ricker 1975). We did not estimate young-of-year (YOY) bass abundances. To determine young-of-year (YOY) and total perch catch per 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.
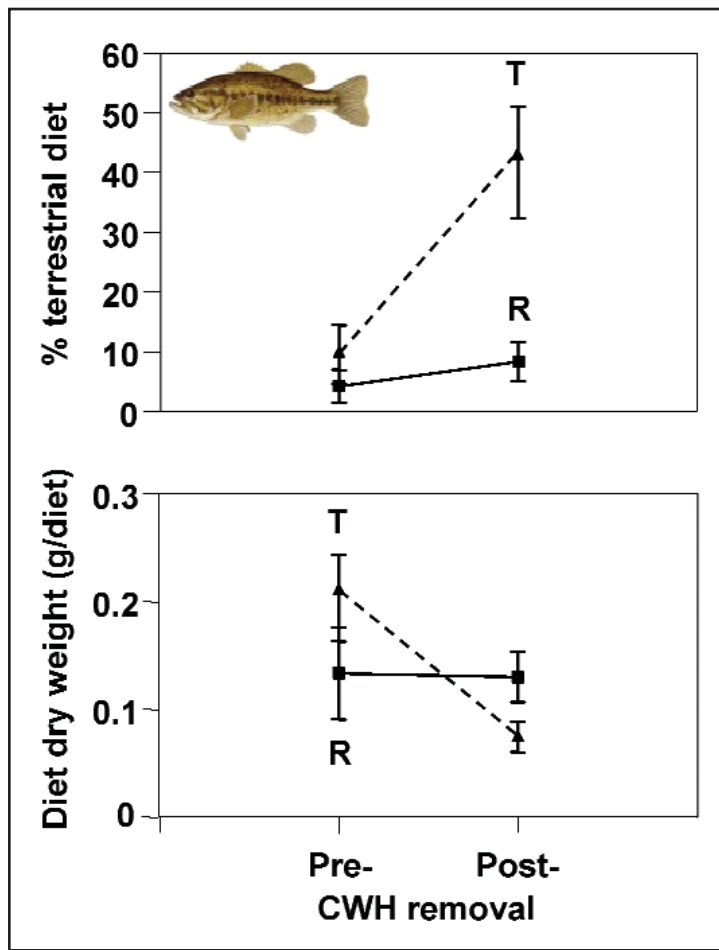
Analysis

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.
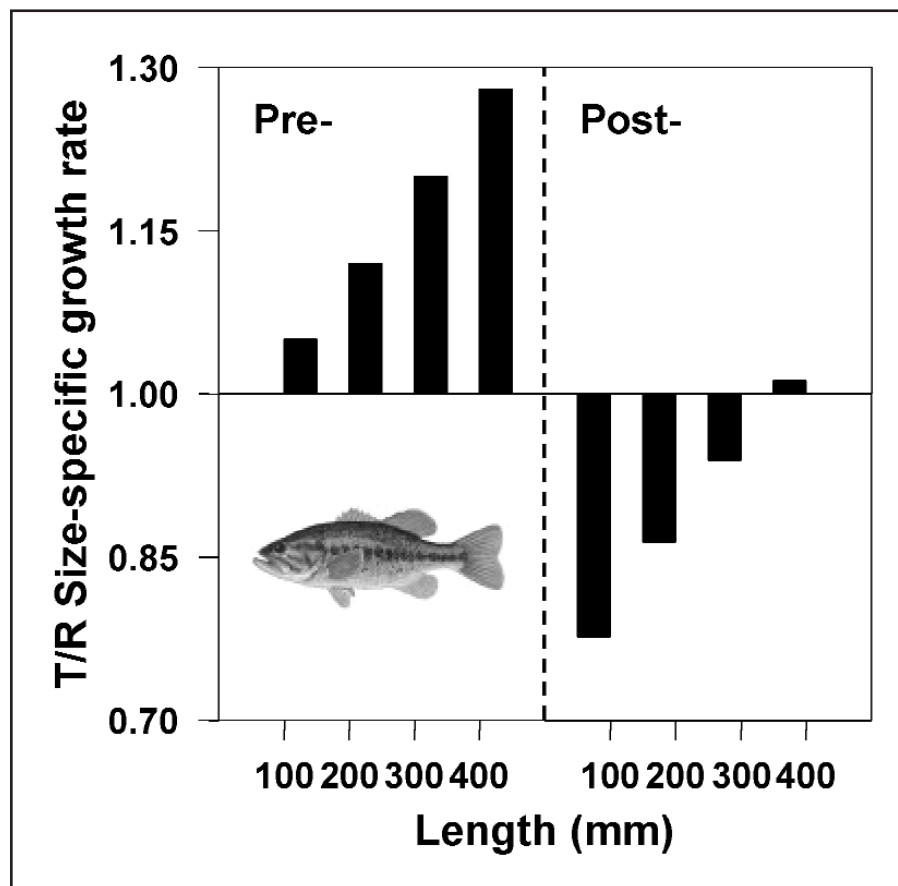
Growth Responses

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.

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.

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 den-

sities. 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

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

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