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# The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*)

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**Abstract** Coarse woody habitat (CWH) may be a critical feature of lakes that influences fish distributions, movement patterns, and feeding habits. We used radio telemetry to examine the role of CWH in determining the movements of largemouth bass (*Micropterus salmoides* Lacepede) in the context of two whole-lake experiments that provided a gradient of four lake basins varying in natural and manipulated CWH. We also conducted diet studies on largemouth bass in these lakes to test for correlates among consumption rate and prey selectivity with bass behavior. Our results indicated that largemouth bass in basins with lower CWH abundances had larger home ranges, spent more time in deep water, were more selective predators, and showed lower consumption rates. Largemouth bass in basins with higher CWH abundances showed the opposite patterns. Low CWH abundances were correlated with a shift in largemouth bass foraging behavior from sit-and-wait to actively searching. This increased activity, coupled with the potential decline of prey fish species in the absence of CWH, may decrease largemouth bass growth potential regardless of the prey type consumed. Our results suggest that lakeshore residential development and associated removals of CWH from lakes may influence fish behavior, while CWH augmentation may reverse some of those changes.

**Keywords** Centrarchidae · Coarse woody habitat · Largemouth bass · Radio telemetry · Structural complexity · Whole-lake experiment

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## Introduction

Structural attributes of aquatic ecosystems may play a large role in determining the distributions, movement patterns, and feeding ecology of fish populations (Scheuerell & Schindler, 2004). Past research has examined the role of aquatic macrophytes in determining home range size and spatial distributions of largemouth bass (*Micropterus salmoide*s Lacepede) (e.g., Essington & Kitchell, 1999). Largemouth bass generally maintain relatively small home ranges (0.2–5.2 ha) in lakes with abundant littoral vegetation (Fish & Savitz, 1983; Mesing & Wicker, 1986; Wildhaber & Neill, 1992) and vegetation tends to

focus largemouth bass distributions in near-shore areas (94–97% of locations less than 3 m deep) (Bain & Boltz, 1992; Essington & Kitchell, 1999; Sass et al., 2006a). While vegetation may play a key role in determining largemouth bass home ranges and distributions, no studies to our knowledge have examined largemouth bass movements in lakes with little vegetation and varying amounts of coarse woody habitat (i.e., logs, branches, trees in the water; CWH) (Newbrey et al., 2005; Sass et al., 2006a).

The relationship between structural habitats and fish movement patterns is ecologically important because a predator's resource use is dictated by home range sizes and spatial distributions, which can ultimately affect aquatic ecosystems through top–down trophic cascading interactions (Carpenter & Kitchell, 1993; Hodgson et al., 1998). Understanding the influences of within-lake structural complexity on fish distributions and movement patterns is also of applied concern as humans continue to alter the riparian and littoral zones of aquatic ecosystems (Newbrey et al., 2005; Sass et al., 2006a, 2006b). For example, the abundance of CWH in lakes is negatively correlated with lakeshore residential development in Upper Michigan, Northern Wisconsin, and Washington State lakes (Christensen et al., 1996; Jennings et al., 2003; Francis & Schindler, 2006; Marburg et al., 2006). Other structural attributes of lakes, such as aquatic macrophytes, show a similar negative correlation with lakeshore residential development (Radomski & Goeman, 2001; Jennings et al., 2003).

The abundance of CWH in lakes may have important consequences for largemouth bass feeding behaviors. Optimal foraging theory states that a predator will maximize energy intake and growth by selecting high energy prey items that minimize energetic losses through foraging and handling costs, while avoiding predation risk (Werner & Hall, 1974; Mittelbach, 1981; Werner & Hall, 1988). Since largemouth bass are keystone species and the apex predator in many systems (Carpenter & Kitchell, 1993), largemouth bass, as well as most fish species, should select a feeding behavior that reflects optimal foraging tenets unless the structural complexity of the system or the forage base dictates otherwise (Hodgson & Kitchell, 1987). Empirical diet information from largemouth bass may provide insight into mechanisms leading to variation in feeding behaviors in lakes with a gradient of habitat complexities and differences in forage bases.

The structural complexity provided by aquatic vegetation and CWH may serve to decrease predator foraging success, provide a focal point for predator–prey interactions in lakes, and cause a shift in largemouth bass foraging behavior (Savino & Stein, 1982; Sass et al., 2006a). For example, largemouth bass forego actively searching for prey and use a sit-and-wait foraging strategy at a threshold level of simulated aquatic vegetation in laboratory studies (Savino & Stein, 1982). The goal of our study was to evaluate largemouth bass movement patterns and feeding habits in the context of two whole-lake experiments that resulted in a gradient of four lake basins (i.e., two separate bodies of water in each lake) varying in natural and manipulated CWH abundances. More specifically, we tested for differences in largemouth bass home range size, minimum activity rate, percentage of time spent in the littoral zone, consumption rate, and dietary breadth among high- and low-CWH treatments in each of the two lakes. Due to the known effects of structure on predator–prey movements and optimal foraging tenets, we hypothesized that largemouth bass in basins with more CWH would move less (i.e., smaller home range) and be less selective predators. With increasing levels of littoral structure, largemouth bass tend to become ambush predators (Savino & Stein, 1982; Sass et al., 2006a). Therefore, this foraging strategy would suggest a smaller home range size and potentially less prey selectivity because prey availability is restricted to the home range of the fish. In this context, we also hypothesized that largemouth bass would adhere to optimal foraging tenets, with respect to maximizing growth potential, given variable feeding behaviors that may result from differences in structural attributes among lakes. With different activity levels (i.e., home range size) of largemouth bass, prey availability and the ability to select energetically profitable prey are dependent upon the size of the individual's foraging arena (Walters & Juanes, 1993). Because largemouth bass are generalist predators and typically consume the most energetically profitable prey item when available within the foraging arena, we predict optimal foraging despite potential changes in feeding behavior caused by the presence or absence of littoral structure (Hodgson & Kitchell, 1987).

## Materials and methods

### Study lakes

We examined largemouth bass movement patterns in two Vilas County, Wisconsin lakes (four basins) with no lakeshore residential development in the summer of 2005. Camp (45°59′58.29″ N 89°43′48.53″ W) and Little Rock lakes (45°59′44.69″ N 89°42′12.76″ W) are separated into two basins (i.e., two separate bodies of water in one lake), creating a treatment and reference basin (Fig. 1). Camp and Little Rock are oligotrophic, seepage lakes with average Secchi disk transparencies exceeding 5 m. Both lakes have maximum depths of 10 m.
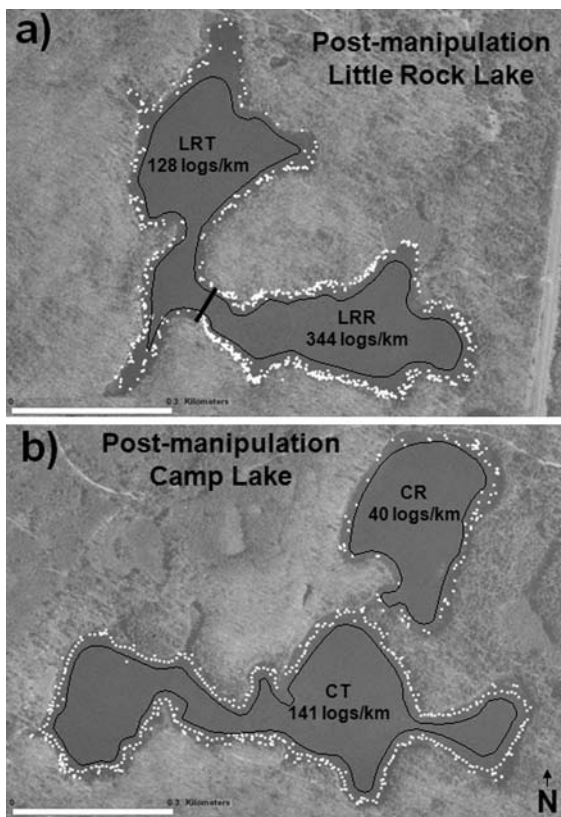


**Fig. 1** Coarse woody habitat (CWH) (logs km$^{-1}$ of shoreline > 10 cm diameter) (white dots) in **a** the treatment (LRT) and reference (LRR) basins of Little Rock Lake after the CWH reduction in LRT in the summer of 2002 and **b** in the treatment (CT) and reference (CR) basins of Camp Lake after the CWH addition in CR in the spring of 2004. The thin black line denotes the 2 m depth contour in each basin. The thick black line in Little Rock Lake represents the double curtain separating LRT and LRR

Little Rock Lake was separated into two basins in 1984 by two poly-vinyl chloride (PVC) curtains, which disallows any movement of fishes or water among basins. Since 1984, Little Rock Lake has been closed to public access and fishing. Little Rock Lake has minimal amounts of aquatic vegetation and about 25% of the surface area is less than 2 m in depth (Fig. 1a). 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 the CWH removal experiment (Sampson, 1999; Hrabik & Watras, 2002). In 2002, about 75% of the littoral zone CWH was removed from the treatment basin of Little Rock Lake (10.5 ha), reducing CWH (logs > 10 cm in diameter) abundances from 475 logs km$^{-1}$ to 128 logs km$^{-1}$ of shoreline (Fig. 1a) (Sass, 2004; Sass et al., 2006b). The reference basin of Little Rock Lake (8.6 ha) remained unchanged (344 logs km$^{-1}$ of shoreline) throughout the study. The fish community of Little Rock Lake is dominated by largemouth bass and yellow perch (*Perca flavescens* Mitchill). However, yellow perch abundances have declined to very low levels following the CWH removal in the treatment basin (Sass et al., 2006b). Black crappie (*Pomoxis nigromaculatus* Lesueur), rock bass (*Ambloplites rupestris* Rafinesque), and central mudminnow (*Umbra limi* Kirtland) are also present at low abundances. Largemouth bass densities were not significantly different among basins prior to the CWH removal (Sass, 2004).

Camp Lake is naturally separated into individual basins by a narrow, shallow channel. Little movement of largemouth bass (<1%, 6 of 820 tagged fish) has been observed among the basins of Camp Lake in previous tagging studies and the current study (G.G. Sass, unpublished data). Camp Lake is a trolling-motor only lake, has a primitive boat launch, and receives minimal fishing pressure. Similar to Little Rock Lake, Camp Lake has sparse aquatic vegetation and about 25% of its surface area is less than 2 m in depth (Fig. 1b). In the spring of 2004, we added over 300 trees (1 for every 10 m of shoreline) to the littoral zone of the treatment basin of Camp Lake (17.6 ha), thus increasing CWH abundances from 41 logs km$^{-1}$ to 141 logs km$^{-1}$ of shoreline (Fig. 1b). Coarse woody habitat (>10 cm in diameter) from various deciduous and coniferous trees was added. We qualitatively scored added CWH for branching complexity on a 0–3 scale with 0 indicating

CWH with no branches and 3 indicating a full crown with attached canopy. Of the added CWH, 8.6% of the CWH scored 0, 20.4% scored 1, 28.4% scored 2, and 42.6% scored 3. The reference basin of Camp Lake (8.5 ha) remained unchanged ( 40 logs km$^{-1}$ of shoreline) throughout the study. Largemouth bass and bluegill (*Lepomis macrochirus* Rafinesque) are the dominant fish species in Camp Lake. Yellow perch, johnny darter (*Etheostoma nigrum* Rafinesque), and Iowa darter (*Etheostoma exile* Girard) comprise the rest of the fish community. Largemouth bass densities were similar in all four basins in 2005 as determined by Chapman-modified continuous Schnabel mark-recapture population estimates (Ricker, 1975) (Table 1). For the purpose of this study, the four basins provided a gradient of CWH abundances listed here from highest to lowest; Little Rock Lake reference (LRR), Camp Lake treatment (CT), Little Rock Lake treatment (LRT), and Camp Lake reference (CR).

Radio telemetry

We surgically implanted radio transmitters (advanced telemetry systems, 3.6 g, 2.4 cm long, 0.7 cm in diameter, 25.5 cm exterior trailing antennae, 55 pulses min$^{-1}$, 18 ms pulse width, ca. 100-day life span), with unique frequencies, into five largemouth bass in each of the four basins ($n = 20$) in June 2005 to allow tracking of positions. Prior to surgery, we held all largemouth bass for 24 h to decrease stress following capture (Cooke et al., 2003; Suski et al., 2003; Suski et al., 2007). Radio transmitters were inserted into the gut cavity on the mid-line of the ventral side of the fish's abdomen, just posterior to the pelvic girdle. All largemouth bass survived the surgical procedure and recovered. After surgery and a 24-h holding period, we released the largemouth bass into their separate basins

and radio tracking began 7-days later to allow sufficient time for healing and for largemouth bass distributions to be established. We conducted all surgical procedures using aseptic techniques. During the study, we were unable to track two largemouth bass in LRR and one largemouth bass in CR due to transmitter failure, transmitter expulsion, mortality due to unknown causes, or harvest by anglers in Camp Lake. One largemouth bass in LRR either lost its transmitter or died of unknown causes as we were able to track the stationary signal over time, yet never observed the fish in the shallow, clear water and were unable to recover the transmitter from the sediment. Data from these three fish were not used in our analyses. All 17 largemouth bass used in our analyses were captured by hook-and-line angling and ranged in size from 300 to 395 mm (0.32–0.73 kg). The mean size of the largemouth bass tracked in Little Rock Lake did not significantly differ among basins (LRT = 369 mm, LRR = 368 mm). In addition, there was no significant difference in the mean size of the largemouth bass tracked among basins in Camp Lake (CT = 333 mm, CR = 327 mm).

We used hand-held loop antennae and a Fieldmaster receiver (advanced telemetry systems) to locate radio-tagged largemouth bass. For each largemouth bass, we located its transmitter signal and then approached the signal until the fish was visually observed or the signal sharply changed direction (Fuller et al., 2005). We selected this method because the low conductivity of the study lakes (Little Rock Lake = 13 μmhos; Camp Lake = 16 μmhos) made the range of the radio signals too short for accurate triangulation. We recorded latitude and longitude for each located largemouth bass using a Garmin model 12XL GPS (~5 m accuracy). We surveyed each basin in a john boat with an electric trolling motor

**Table 1** Experimental and biological attributes of Little Rock and Camp lakes, Vilas County, Wisconsin, USA, with the number of adult largemouth bass (*Micropterus salmoides* Lacepede) tracked, diet breadth, consumption, and population estimates for each basin

| Lake | Basin (treatment) | Surface area (ha) | Logs km$^{-1}$ of shoreline | No. of LMB tracked | Diet breadth | Consumption (g diet$^{-1}$) | LMB density with 95% CI (no. ha$^{-1}$) |
|------|-------------------|-------------------|------------------------------|---------------------|--------------|------------------------------|------------------------------------------|
| Little Rock | LRT (− wood) | 10.5 | 128 | 5 | 3.9 | 0.091 | 98 (82–121) |
| | LRR (Control) | 8.6 | 344 | 3 | 2.9 | 0.154 | 106 (85–134) |
| Camp | CT (+ wood) | 17.6 | 141 | 5 | 2.2 | 0.144 | 64 (47–95) |
| | CR (Control) | 8.5 | 40 | 4 | 1.95 | 0.066 | 86 (49–229) |

LRT = Little Rock Lake treatment, LRR = Little Rock Lake reference, CT = Camp Lake treatment, CR = Camp Lake reference, CI = Confidence interval, and LMB = Largemouth bass

from 7 July 2005 to 25 August 2005 using the cyclic sampling design described below. Because largemouth bass home range sizes may change seasonally, our tracking was limited to a 7-week summer period to reduce any bias associated with spawning and overwintering movements.

We located largemouth bass according to a cyclic sampling schedule based on a 3/7 cycle (Clinger & Van Ness, 1976; Burrows et al., 2002). This design allowed us to efficiently measure both fine-scale and broad-scale patterns of largemouth bass movements. Each week, for 7 weeks, we located the largemouth bass midmorning on Monday, Tuesday, and Thursday (i.e., three sampling days per 7 days = 3/7 cycle). In addition, on Tuesdays, we located each largemouth bass 12-h later than when located midmorning. On Thursdays, we located each largemouth bass at 4, 6, or 8 h time intervals for 24-h. This sampling design resulted in about 50 marked locations per largemouth bass at a variety of temporal lags.

### Telemetry data analyses

We used an adaptive kernel-based estimation procedure to calculate the home range size of each largemouth bass. We chose this method because it is non-parametric and not affected by auto-correlated data (Kernohan et al., 2001). The input into the kernel estimator is the measured locations for each individual largemouth bass. The estimated value of the utilization distribution (UD) at an observed location is calculated by:

$$\hat{f}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - Xi}{h}\right] \qquad (1)$$

where $\hat{f}(x)$ is the estimated probability density function, or UD, $n$ the number of locations, $h$ the smoothing parameter or bandwidth, $X$ contains the $x$ and $y$ coordinates for the $n$ observed locations, $x$ the point at which the kernel estimate is calculated, and $K$ the kernel function (Worton, 1989). The estimated home range area can be thought of as the sum of $n$ separate kernel functions, each centered at a marked location (Silverman, 1986). The bandwidth ($h$ value) controls the width of the individual kernels, and therefore, the amount of smoothing applied to the home range estimation. Large bandwidth values result in greater smoothing of the data, while a small

bandwidth value creates less smoothing and smaller kernels. A different $h$ value, depending upon the distribution of the fish's locations, is used to calculate each individual home range. A common method to calculate the bandwidth value for each fish is to use least squares cross validation (LSCV), which minimizes error between the estimated and true density (Kernohan et al., 2001). We used the LSCV method to calculate the $h$ value (using the statistical software package R) for individual largemouth bass (Kernohan et al., 2001). We then calculated each fish's home range size, using the $h$ value and the marked locations of that largemouth bass, in the statistical software package Biotas 1.03. The home range size of all the largemouth bass in each basin were then averaged to give a mean home range size per basin. For the purpose of this study, the largest possible home range size corresponded to the surface area of the basin. No home range was defined as a fish that was observed in the same location throughout the 7-week study period.

We conducted separate two-tailed $t$-tests for each lake to test for the effects of high-and low-CWH treatments on average largemouth bass home range sizes with the null hypothesis of no difference in average home range size among basins ($\alpha = 0.05$). We also used simple linear regression to test for a relationship between mean home range size and CWH abundance with the null hypothesis of no change in slope with increasing CWH abundances among the basins of Camp and Little Rock lakes (ANOVA; $\alpha = 0.05$) due to the similarity of the study systems. CWH abundance was reciprocally transformed to satisfy the assumptions of ANOVA (Draper & Smith, 1998). While our observations among basins were not independent, this regression analysis was statistically valid because we did not use the fitted regression model to make inferences to lakes not in our study (Hurlbert, 1984). Our regression analysis was thus only used to describe relationships between largemouth bass behavior and CWH in our study lakes, and should not be used to make predictions as to the home range size of largemouth bass in other lakes that vary in CWH abundance.

We also calculated the average minimum activity rate (m h$^{-1}$) for largemouth bass in each basin. Because we located each bass at a minimum of every 4 h, we defined this metric as a minimum activity rate

to account for longer movements that may have occurred within the 4-h untracked period. For individual largemouth bass, we calculated the minimum movement in every 4-h time interval and standardized this rate among fish as the minimum movement per hour. The movement per hour observed for each bass was then averaged to provide the mean minimum distance moved per hour by largemouth bass in each basin. A separate two-tailed *t*-test for each lake was used to test for the effects of differing CWH densities on largemouth bass minimum activity rates with the null hypothesis of no difference in minimum activity rate among basins ($\alpha = 0.05$).

Lastly, we used the radio telemetry data to examine bathymetric spatial distributions of largemouth bass throughout the basins. Largemouth bass locations were described as either being located in ≤2 m of water or in water >2 m. The 2 m depth contour generally corresponded to the edge of the littoral refuge in each basin. Coarse woody habitat in water >2 m in depth was rare in both study lakes (G.G. Sass, personal observation). We recorded the total depth of the water column for every relocated largemouth bass in each tracking period and reported the mean percent of time all largemouth bass in each basin spent in shallow water. We used separate two-tailed *t*-tests for each lake to test for differences in the percent of observations where largemouth bass were located in water ≤2 m deep among basins with the null hypothesis of no difference in the percent of locations observed ≤2 m deep among basins ($\alpha = 0.05$).

Diet analyses

We collected diet information from largemouth bass at biweekly intervals during May–September, 2004–2005 in each basin of Camp and Little Rock lakes. Although our telemetry study was conducted in 2005, we combined post-CWH manipulation diet data to provide a broader picture of largemouth bass diet composition in each basin (LRR, $n = 163$; LRT, $n = 167$; CR, $n = 108$; CT, $n = 119$). All largemouth bass were collected by hook-and-line angling because the low conductivity of the water precluded effective electrofishing. We determined diet composition by performing gastric lavage on at least 10 largemouth bass (range: 10–20) on each sampling occasion in each basin (Seaburg, 1957; Hodgson & Kitchell, 1987).

Largemouth bass sizes ranged from 182 to 455 mm and 162 to 411 mm in Camp and Little Rock lakes, respectively. Although our radio-tagged largemouth bass were larger individuals (300–395 mm), ontogenetic diet shifts to piscivory in largemouth bass may occur in the first summer and are generally complete by the second summer of life in north temperate lakes (Post, 2003). The minimum size of the largemouth bass used in our diet analyses were 2–3-year-old individuals; therefore, our radio-tagged largemouth bass should be representative of the fish population sampled for diets (Sass, 2004). Diet items were separated into major taxonomic categories (e.g., Amphipoda, Coleoptera, Diptera, fish, Odonata, terrestrial invertebrate, terrestrial vertebrate, and Trichoptera), enumerated, and dried to determine the dry mass proportion of each prey item in the diet.

An index of absolute importance (IAI) was calculated for each prey category as follows:

$$\text{IAI}_a = \%N_a + \%W_a + \text{FO}_a \tag{2}$$

where $\%N$ was the percentage of the total number of food items represented by food type a, $\%W$ the percentage weight (grams of dry biomass) of each food item a of the total weight of foods eaten, and FO the frequency of occurrence of each food type a (the percentage of fish that eat that food type) (George & Hadley, 1979). We then used IAI values to calculate an index of relative importance (IRI) for each prey item:

$$\text{IRI}_a = 100 * \frac{(\text{IAI}_a)}{(\sum \text{IAI}_a)} \tag{3}$$

where a is the specific food item and the summation in the denominator is taken over all food items. The range of IRI values for any diet was 0–100 (Hodgson & Kitchell, 1987). We calculated diet breadth (*B*) for largemouth bass in each basin following Levins (1968):

$$B = \frac{1}{\sum p_i^2} \tag{4}$$

where $p_i$ is the fraction of total diet mass represented by item i and the summation is over 1. This index is minimized at 1.0 when only one prey type is found in the diet and is maximized at *n*, where *n* is the total number of prey types, each representing an equal proportion of the diet (Schindler et al., 1997). Diet

breadth was calculated to test whether prey proportions and diversity were correlated with CWH abundances and largemouth bass home range sizes among basins. We used separate two-tailed $t$-tests for each lake to test for differences in largemouth bass consumption rates among basins with the null hypothesis of no difference in consumption rates among the high- and low-CWH treatments in each lake ($\alpha = 0.05$). Consumption rate was $\log_e$ transformed to satisfy the assumption of normality for $t$-tests.

## Results

Average home range sizes for largemouth bass decreased significantly with increasing levels of CWH among basins (home range size (ha) $= 0.443 + 108.57 \cdot$ CWH abundance$^{-1}$; $n = 4$; df $= 1,2$; $F = 57.85$; $P = 0.017$; $R^2 = 0.97$) (Fig. 2). The home range size of largemouth bass in LRT ($n = 5$) averaged 1.57 ha, while largemouth bass in LRR ($n = 3$) averaged 0.69 ha (Fig. 3). The home range size of largemouth bass in CT ($n = 5$) and CR ($n = 4$) averaged 1.03 and 3.13 ha, respectively (Fig. 3). Average largemouth bass home range size
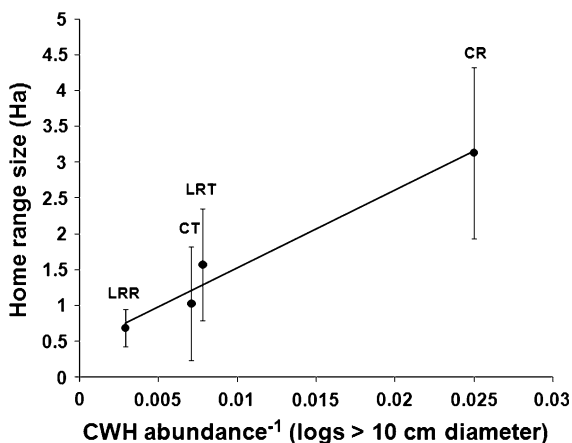


**Fig. 2** Simple linear regression of average home range size for largemouth bass (*Micropterus salmoides* Lacepede) versus the reciprocal of the amount of coarse woody habitat (CWH) (logs km$^{-1}$ > 10 cm diameter) in each basin studied (home range size (ha) $= 0.443 + 108.57 \cdot$ CWH abundance$^{-1}$; $n = 4$; df $= 1,2$; $F = 57.85$; $P = 0.017$; $R^2 = 0.97$). Error bars denote the standard error about the mean. CR = Camp Lake reference basin, CT = Camp Lake treatment basin, LRR = Little Rock Lake reference basin, LRT = Little Rock Lake treatment basin
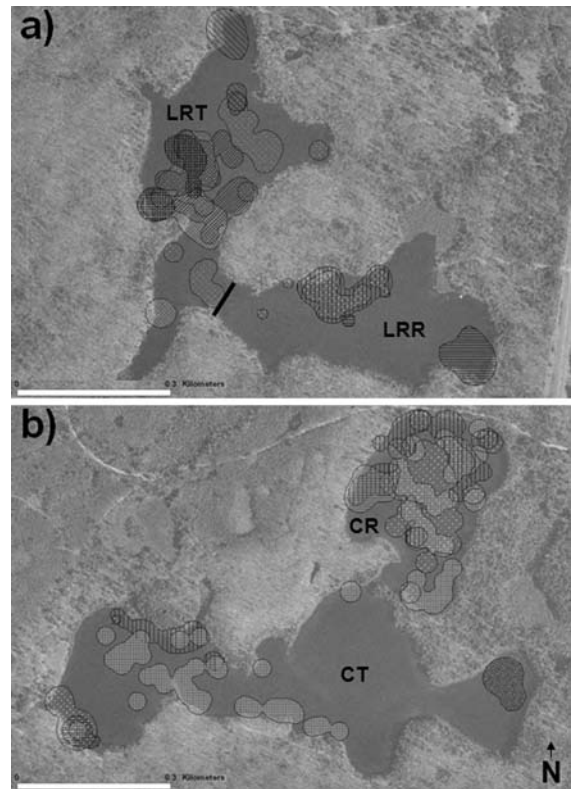


**Fig. 3** Home ranges of largemouth bass (*Micropterus salmoides* Lacepede) in the **a** treatment (LRT) ($n = 5$) and reference (LRR) ($n = 3$) basins of Little Rock Lake and **b** the treatment (CT) ($n = 5$) and reference (CR) ($n = 4$) basins of Camp Lake. Home ranges for individual bass are delineated by separate patterns. Overlap of individual home ranges with land were due to home ranges being estimates of probability, not physical space

did not significantly differ among treatments in each lake. Overlap of individual home ranges with land was due to home ranges being estimates of probability, not physical space (Fig. 3).

Largemouth bass average minimum activity rates were significantly lower in the high-CWH treatments compared to the low-CWH treatments in each lake (LRR vs. LRT, $n = 78$, df $= 76$, $t = 2.26$, $P = 0.03$; CR vs. CT, $n = 90$, df $= 88$, $t = 2.21$, $P = 0.03$). Average minimum activity rates for largemouth bass were LRR ($8.09 \pm 1.86$ m h$^{-1}$), LRT ($13.98 \pm 1.65$ m h$^{-1}$), CR ($18.00 \pm 1.76$ m h$^{-1}$), and CT ($12.05 \pm 1.96$ m h$^{-1}$).

Greater amounts of CWH in a basin resulted in more observations of largemouth bass located in the littoral zone of each lake (LRR vs. LRT, $n = 8$, df $= 6$, $t = 2.91$, $P = 0.03$; CR vs. CT, $n = 9$, df $= 7$, $t = 3.23$, $P = 0.01$). Largemouth bass in

LRT were located in ≤2 m of water during 58% of the recorded locations, while largemouth bass in LRR were found in shallow water 69% of the time. Largemouth bass in CT and CR were found in shallow water 94% and 46% of the time, respectively.

Diet breadth and consumption rates increased in largemouth bass populations across the gradient of lakes from low to high amounts of CWH. Largemouth bass were more selective predators in CR (largest home range size, least CWH) compared to largemouth bass in CT and LRR (smallest home range size, most CWH) (Table 1). In contrast to this pattern, diet breadth was greatest for largemouth bass in LRT. Largemouth bass consumption rates were significantly greater in the high-CWH treatments compared to the low-CWH treatments in each lake ($\log_e$ LRR vs. $\log_e$ LRT, $n = 330$, df = 328, $t = 2.16$, $P = 0.03$; $\log_e$ CR vs. $\log_e$ CT, $n = 227$, df = 225, $t = 1.92$, $P = 0.05$). Prey biomass per largemouth bass diet (a proxy for consumption rate) increased from 0.066 g diet$^{-1}$ in CR largemouth bass to 0.154 g diet$^{-1}$ in LRR largemouth bass. Intermediate consumption rates were observed in largemouth bass from LRT (0.091 g diet$^{-1}$) and CT (0.144 g diet$^{-1}$) (Table 1).

Fish and odonate nymphs dominated the diets of largemouth bass in all basins, but differed in importance among lakes. Index of relative importance values for fish prey approached 60% for largemouth bass in CR (fish IRI = 58%) and CT (fish IRI = 59%). Largemouth bass diets were more dominated by odonate larvae than fish in LRR (Odonata IRI = 38%) and LRT (Odonata IRI = 25%) (LRR fish IRI = 33%, LRT fish IRI = 23%). Largemouth bass diets in LRT were also supplemented by terrestrial invertebrate and vertebrate prey (terrestrial IRI = 23%).

## Discussion

Our study suggests that variability in largemouth bass home range sizes, spatial distributions, and feeding behaviors among lakes may be influenced by CWH. Largemouth bass home range sizes decreased significantly with increasing CWH abundances and average minimum activity rates were lower in basins with greater densities of CWH. Our inability to detect significant differences in largemouth bass home range sizes among basins in each lake may have been a result

of low statistical power (Carpenter et al., 1995). We were only able to track up to five largemouth bass in each basin and lost several individuals, which further decreased our statistical power to detect effects. Previous studies of largemouth bass home range sizes and spatial distributions suggest that movements are often influenced by aquatic vegetation (Bain & Boltz, 1992; Demers et al., 1996; Essington & Kitchell, 1999). Our results show similar patterns in largemouth bass movements in lakes with varying levels of CWH. According to Savino & Stein (1982), largemouth bass use a sit-and-wait foraging strategy at high densities of simulated aquatic vegetation and a cruising strategy with decreased levels of structure. Although population density and size–structure may also influence fish movement behaviors, largemouth bass densities and size–structure were not significantly different among treatments suggesting that these factors were not important drivers of differences in movement behaviors among basins. Therefore, the amount of littoral zone structure present in an aquatic ecosystem may be a major factor dictating which foraging strategy a predator uses.

Greater densities of CWH were associated with more observations of largemouth bass in shallow water. The predominant usage of shallow water by largemouth bass in CT (94% of locations ≤2 m) is likely attributable to the amount of complex CWH available (Newbrey et al., 2005). Because 100 logs km$^{-1}$ of shoreline were added to this basin in 2004, greater amounts of structurally complex CWH was available that had not been degraded or buried in sediment compared to LRR. Therefore, our results also suggest that largemouth bass distributions are affected by CWH abundances. The distributions of largemouth bass may be a result of the tradeoff observed between foraging strategies and available littoral zone structure. In concert, perturbations to littoral structure may alter fish behaviors from what would normally be observed in lakes rich with CWH and aquatic macrophytes.

Similar to other studies, the distributions of largemouth bass among basins in our study were variable and likely dependent upon prey distributions. For example, Mesing & Wicker (1986) reported that largemouth bass were consistently observed in both the littoral and pelagic zone, while other studies found that largemouth bass spent nearly all of their time in the littoral zone or directly adjacent to it (Winter, 1977; Essington & Kitchell, 1999). The

study that reports largemouth bass movements in shallow and deep water was from a lake in Florida, which contained both littoral and pelagic prey species. The other studies were in Minnesota and Michigan lakes, which contained prey species generally associated with the littoral zone. Differences in the distributions of largemouth bass among studies may be caused by different prey availabilities and distributions, which can be linked to the presence of littoral structure. With less CWH, prey species may distribute more variably throughout the water column, while high CWH abundances may focus prey in shallow, refuge areas (Sass et al., 2006a; Lewin et al., 2004). For example, Sass et al. (2006a) showed that predation by largemouth bass was focused on the edge of littoral refuge habitats in lakes with high structural complexity and was more diffuse in less structurally complex lakes. In addition, the Sass et al. (2006a) study used tethering of prey to infer largemouth bass distributions in two different lakes than those presented here and found similar results.

Assuming that our radio-tagged fish were indicative of the overall largemouth bass population, largemouth bass with the largest home range sizes were the most selective predators in our study. However, diet breadth in LRT was unusually high compared to the other basins. The treatment basin of Little Rock Lake was subjected to a whole-lake reduction of CWH in 2002, which caused the collapse of the dominant forage fish, yellow perch (Sass, 2004; Sass et al., 2006b). The loss of CWH in LRT likely resulted in a switch in largemouth bass foraging behavior to actively searching, but also caused a decrease in prey selectivity with the loss of the dominant forage fish population. The collapse of the yellow perch population in LRT resulted in a shift in largemouth bass diets from primarily fish to terrestrial sources of prey (Sass et al., 2006b). Given equivalent water temperatures among systems, fish growth is bioenergetically determined by consumption rates, the energy density of prey consumed, and activity costs (Hanson et al., 1997). Therefore, fishes using different optimal foraging strategies may still grow at equivalent rates. For example, a fish that expends little energy foraging and non-selectively feeds on low energy prey at high rates may still grow equivalently to a predator that is actively searching (i.e., high activity costs) and selectively consuming lower amounts of energy-rich prey. Largemouth bass

consumption rates were negatively correlated with home range size among basins. Larger home range size and increased prey selectivity resulted in lower consumption rates by largemouth bass in CR and LRT. In contrast, largemouth bass in CT and LRR were less selective, but had higher consumption rates. The lower consumption rates observed in the largemouth bass of CR and LRT do not appear to be strongly correlated with a reduction in prey densities. Bluegill populations remain robust in both basins of Camp Lake, and macroinvertebrate densities did not change and largemouth bass switched to a more terrestrial diet in LRT following the CWH removal (Sass et al., 2006b; Helmus and Sass, 2008). Combinations of lower activity and higher consumption rates may increase growth potential for largemouth bass in the presence of CWH and an energy-rich forage base (Schindler et al., 2000; Sass et al., 2006b). For example, Schindler et al. (2000) reported higher size-specific growth rates in bluegill and largemouth bass from lakes with greater amounts of CWH, while Sass et al. (2006b) observed declines in largemouth bass growth rates following the whole-lake removal of CWH described in the present study.

Our findings supported the prediction that largemouth bass in CWH-rich basins would have smaller home range sizes and be less selective predators. The presence of CWH, similar to simulated aquatic macrophytes, appears to create ambush points for largemouth bass (sit-and-wait foraging strategy) (Savino & Stein, 1982; Sass et al., 2006a). Although this strategy may negatively influence selectivity (i.e., selectivity of prey items is restricted to availability within the home range), increased consumption rates of marginal prey may still provide for optimal growth due to the lack of energy loss associated with actively searching for prey (Hanson et al., 1997). Our observations also supported the prediction of optimal foraging by largemouth bass given differences in movement behaviors associated with various levels of littoral CWH. Despite the foraging strategy used, our empirical diet studies suggest optimal foraging in terms of growth by largemouth bass either having a: (1) small home range and minimum activity rate (i.e., little energy loss due to activity), being a less selective predator, and maintaining higher consumption rates; or (2) large home range and minimum activity rate (i.e., high-energy loss due to activity), being a more selective predator, and maintaining

lower consumption rates. According to bioenergetics principles, these two foraging strategies would maximize growth potential given that littoral structure appears to alter the type of feeding behavior used.

The results of our study provide further support that CWH is a critical feature of lakes (Schindler et al., 2000; Newbrey et al., 2005; Sass et al., 2006b). Removal of CWH, which is commonly observed as a consequence of the lakeshore residential development process, may alter home ranges, distributions, and feeding habits of largemouth bass. In addition to effects on largemouth bass, these changes in home range size and movement patterns may also have negative consequences for small fishes and macroinvertebrates (Sass et al., 2006b). Our results further suggest that CWH augmentation may reverse some of the negative effects of anthropogenic CWH removal on fish behavior. Future research should be aimed to track a greater number of largemouth bass in a larger number of systems over a gradient of fish sizes to determine intra-population, size-specific, and threshold effects of CWH on fish home ranges, distributions, and feeding habits.

# References

Bain, M. B. & S. E. Boltz, 1992. Effect of aquatic plant control on the microdistribution and population characteristics of largemouth bass. Transactions of the American Fisheries Society 121: 94–103.

Burrows, S. N., S. T. Gower, M. K. Clayton, D. S. Mackay, D. E. Ahl, J. M. Norman & G. Diak, 2002. Application of geostatistics to characterize leaf area index (LAI) from flux tower to landscape scales using a cyclic sampling design. Ecosystems 5: 667–679.

Carpenter, S. R. & J. F. Kitchell, 1993. The Trophic Cascade in Lakes. Cambridge University Press, Cambridge, England.

Carpenter, S. R., P. Cunningham, S. Gafny, A. Munoz-Del-Rio, N. Nibbelink, M. Olson, T. Pellett, C. Storlie & 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 & S. R. Carpenter, 1996. Impacts of lakeshore development on coarse woody debris in north temperate lakes. Ecological Applications 6: 1143–1149.

Clinger, W. & J. W. Van Ness, 1976. On unequally spaced time points in time series. Annals of Statistics 4: 736–745.

Cooke, S. J., B. D. S. Graeb, C. D. Suski & K. G. Ostrand, 2003. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: Case study of a novice and experienced fish surgeon. Journal of Fish Biology 62: 1366–1380.

Demers, E., R. S. McKinley, A. H. Weatherley & D. J. McQueen, 1996. Activity patterns of largemouth and smallmouth bass determined with electromyogram biotelemetry. Transactions of the American Fisheries Society 125: 434–439.

Draper, N. R. & H. Smith, 1998. Applied Regression Analysis, 3rd ed. Wiley, New York.

Essington, T. E. & J. F. Kitchell, 1999. New perspectives in the analysis of fish distributions: A case study on the spatial distribution of largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 56: 52–60.

Fish, P. A. & J. Savitz, 1983. Variations in home ranges of largemouth bass, yellow perch, bluegills and pumpkin seeds in an Illinois lake. Transactions of the American Fisheries Society 112: 147–153.

Francis, T. B. & D. E. Schindler, 2006. Degradation of littoral habitats by residential development: Woody debris in lakes of the Pacific Northwest and Midwest, United States. Ambio 35: 274–280.

Fuller, M. R., J. J. Millspaugh, K. E. Church & R. E. Kenward, 2005. Wildlife radiotelemetry. In Braun, C. E. (ed.), Techniques for Wildlife Investigations and Management, 6th ed. The Wildlife Society, Maryland: 377–417.

George, E. L. & W. F. Hadley, 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108: 253–261.

Hanson, P. C., T. B. Johnson, D. E. Schindler & J. F. Kitchell, 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Institution, Madison, Wisconsin.

Helmus, M. R. & G. G. Sass, 2008. The rapid effects of a whole-lake reduction of coarse woody debris on fish and benthic macroinvertebrates. Freshwater Biology 53: 1423–1433.

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

Hodgson, J. R., D. E. Schindler & X. He, 1998. Homing tendency of three piscivorous fishes in a north temperate lake. Transactions of the American Fisheries Society 127: 1078–1081.

Hrabik, T. R. & 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.

Hurlbert, S. H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187–211.

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

Kernohan, B. J., R. A. Gitzen & J. J. Millspaugh, 2001. Analysis of animal space use and movements. In Millspaugh, J. J. & J. M. Marzluff (eds), Radio Tracking and Animal Populations. Academic Press, California: 126–164.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, New Jersey.

Lewin, W. C., N. Okun & T. Mehner, 2004. Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. Freshwater Biology 49: 410–424.

Marburg, A. E., M. G. Turner & T. K. Kratz, 2006. Natural and anthropogenic variation in coarse wood among and within lakes. Journal of Ecology 94: 558–568.

Mesing, C. L. & A. M. Wicker, 1986. Home range, spawning migrations, and homing of radio-tagged Florida largemouth bass in two central Florida lakes. Transactions of the American Fisheries Society 115: 286–295.

Mittelbach, G. G., 1981. Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. Ecology 62: 1370–1386.

Newbrey, M. G., M. A. Bozek, M. J. Jennings & J. E. Cook, 2005. Branching complexity and morphological characteristics of coarse woody structure as lacustrine fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 69: 2110–2123.

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

Radomski, P. & T. J. Goeman, 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. Bulletin of the Fisheries Research Board of Canada, Government of Canada, Ottawa.

Sampson, C. J., 1999. Aquatic chemistry of Little Rock Lake, Wisconsin, during acidification and recovery. Dissertation, University of Minnesota-Twin Cities.

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

Sass, G. G., C. M. Gille, J. T. Hinke & J. F. Kitchell, 2006a. Whole lake influences of littoral structural complexity and prey body morphology on fish predator-prey interactions. Ecology of Freshwater Fish 15: 301–308.

Sass, G. G., J. F. Kitchell, S. R. Carpenter, T. R. Hrabik, A. E. Marburg & M. G. Turner, 2006b. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Fisheries 31: 321–330.

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

Scheuerell, M. D. & 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 & J. F. Kitchell, 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia 110: 592–600.

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

Seaburg, K. G., 1957. A stomach sampler for live fish. Progressive Fish-Culturist 19: 137–139.

Silverman, B. W., 1986. Density Estimation for Statistics and Data Analysis. Chapman and Hall, London.

Suski, C. D., S. S. Killen, M. B. Morrissey, S. G. Lund & B. L. Tufts, 2003. Physiological changes in largemouth bass caused by live-release angling tournaments in Southeastern Ontario. North American Journal of Fisheries Management 23: 760–769.

Suski, C. D., S. J. Cooke & B. L. Tufts, 2007. Failure of low-velocity swimming to enhance recovery from exhaustive exercise in largemouth bass (*Micropterus salmoides*). Physiological and Biochemical Zoology 80: 78–87.

Walters, C. J. & F. Juanes, 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50: 2058–2070.

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

Werner, E. E. & D. J. Hall, 1988. Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. Ecology 69: 1352–1366.

Wildhaber, M. L. & W. H. Neill, 1992. Activity and distribution of northern and Florida largemouth bass in a Texas impoundment. Journal of Freshwater Ecology 7: 293–302.

Winter, J. D., 1977. Summer home range movements and habitat use by 4 largemouth bass in Mary Lake, Minnesota. Transactions of the American Fisheries Society 106: 323–330.

Worton, B. J., 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70: 164–168.