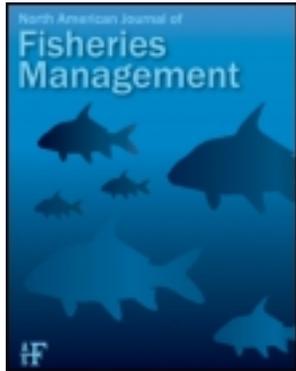


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Largemouth Bass Nest Site Selection in Small, North Temperate Lakes Varying in Littoral Coarse Woody Habitat Abundances

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MANAGEMENT BRIEF

Largemouth Bass Nest Site Selection in Small, North Temperate Lakes Varying in Littoral Coarse Woody Habitat Abundances

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Abstract

Coarse woody habitat (CWH) in the littoral zone is an important habitat feature in freshwater systems and has been suggested to influence nest density and nest site selection by black basses *Micropterus* spp. (e.g., largemouth bass *M. salmoides* and smallmouth bass *M. dolomieu*). To test for a relationship between nest site selection or nest density and the abundance of littoral CWH, we monitored largemouth bass nest site selection in the littoral zones of two small, northern Wisconsin lakes (comprising a total of three separated basins) for three consecutive spawning seasons. Our study sites varied in natural and manipulated abundances of CWH; spawning seasons before and after a whole-basin CWH reduction or a whole-basin CWH addition were examined. Within-basin analysis provided some evidence that local variation in CWH abundance influenced local nest density; however, this relationship was only significant for one basin in a single season. Among basins and across seasons, we observed a positive but nonsignificant effect of littoral CWH density on nest density and inconsistent responses to the CWH manipulations. Although littoral CWH is an important habitat feature influencing fish populations, communities, and life histories, our results suggest that CWH did not directly limit largemouth bass nest densities and was not a strong driver of nest site selection in these lakes. Nevertheless, policies allowing human-mediated removals of CWH from freshwater systems may still be detrimental to fish communities and other taxa that are dependent upon CWH.

Coarse woody habitat (CWH) density in the littoral zone is negatively correlated with lakeshore residential development in northern Wisconsin, upper Michigan, and Washington State lakes (Christensen et al. 1996; Jennings et al. 2003; Francis

and Schindler 2006; Marburg et al. 2006). Largemouth bass *Micropterus salmoides* are sensitive to reductions in CWH and increases in lakeshore residential development, displaying changes in foraging behavior, diet composition, home range size, and growth rate (Schindler et al. 2000; Sass et al. 2006a, 2006b; Ahrenstorff et al. 2009; Gaeta et al. 2011). Coarse woody habitat and other littoral structure have also been suggested to be important for nest site selection, nest density, and nesting success of largemouth bass and smallmouth bass *M. dolomieu* (Vogele and Rainwater 1975; Hoff 1991; Nack et al. 1993; Annett et al. 1996; Hunt and Annett 2002; Hunt et al. 2002; Saunders et al. 2002; Wills et al. 2004). Recent studies have observed a negative influence of shoreline development on nest site selection (Reed and Pereira 2009) and nesting success (Wagner et al. 2006). Collectively, this evidence suggests that the absence or removal of littoral structure may preclude sexually mature male black bass *Micropterus* spp. from spawning, thus potentially limiting young-of-the-year production (Hoff 1991; Hunt and Annett 2002). To address the role of littoral CWH at the whole-basin scale, we analyzed nest density for three largemouth bass populations during spawning seasons before and after a well-documented whole-basin addition of littoral CWH and a separate whole-basin reduction of littoral CWH (Sass et al. 2006b; Helmus and Sass 2008).

Among studies that have experimentally manipulated littoral structure to examine nesting by black basses, few have been conducted in systems where the influence of changes in littoral structure on nesting can be considered at the scale of the entire

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population (but see Hoff 1991 for smallmouth bass). Studies that have focused on a subset of the available littoral habitat or localized habitat manipulations (or both) within larger systems provide strong evidence for a positive influence of littoral structure on black bass nest density (Vogele and Rainwater 1975; Hunt and Annett 2002; Hunt et al. 2002; Wills et al. 2004). Although the absence of local littoral structure may preclude sexually mature individuals from spawning, thus potentially limiting young-of-the-year recruitment, it is also possible that individual black bass select optimal nest sites based on a number of factors including littoral structure but do not forgo spawning based on the absence of littoral structure. Given that largemouth bass can persist in a diversity of habitats that vary widely in the availability of littoral structure, studies that consider population-level responses of habitat alterations may provide information at a more appropriate scale for use by managers that are interested in maximizing young-of-the-year production. Considering the suggested influences of littoral structure on black bass nesting and reproduction, we tested for the influence of CWH abundance at two scales. To test whether variation in littoral habitat drives nest site selection within a basin, we analyzed the relationship between local (within-basin) levels of littoral CWH density and largemouth bass nest density. To test whether natural or anthropogenic variation in whole-basin CWH density influences whole-basin nest density, we analyzed the relationship between nest density and CWH density among basins and across spawning seasons.

STUDY SITES

We studied the largemouth bass populations of Little Rock Lake (45°59'44.69"N, 89°42'12.76"W) and the southern basin

of Camp Lake (45°59'58.29"N, 89°43'48.53"W), which are located about 4 km apart in Vilas County, Wisconsin. These oligotrophic seepage lakes are surrounded by mixed northern hardwood–conifer forests and have no lakeshore residential development. The littoral zones of the lakes are dominated by sand, silt, and leafy detritus; some areas consist of coarser substrate (i.e., gravel, cobble, and boulders). In the mid-1980s, an impermeable curtain was used to partition Little Rock Lake into two basins for purposes of conducting a whole-basin acidification experiment. After the experiment, the acidified basin was allowed to recover, and by the time of our study the aquatic community of the acidified basin had converged with that of the reference basin (Frost et al. 1999; Hrabik and Watras 2002). The southern basin of Camp Lake is connected to a smaller northern basin by a shallow, narrow channel, but minimal movement of largemouth bass has been observed between basins (Ahrenstorff et al. 2009).

Prior to our CWH manipulation, Little Rock Lake contained densities of littoral CWH (logs with a diameter > 10 cm and a length > 150 cm) that were well above median levels for undeveloped lakes in northern Wisconsin (median = 66.3 logs/km; Marburg et al. 2006), whereas Camp Lake contained little natural CWH (Table 1). After the largemouth bass spawning season in summer 2002, about 75% of the littoral CWH was removed from the western basin of Little Rock Lake (Little Rock–Reduction), resulting in a CWH density of 128 logs/km in the 2003 and 2004 spawning seasons (Sass et al. 2006b; Ahrenstorff et al. 2009). Prior to the spawning season in spring 2004, over 300 trees were added (1 tree for every 10 m of shoreline) to the littoral zone of the southern basin of Camp Lake (Camp–Addition), thus increasing the CWH density

TABLE 1. Whole-basin estimates of littoral coarse woody habitat (CWH) density, adult largemouth bass density (with 95% confidence interval in parentheses), and largemouth bass nest density observed in three Wisconsin basins: the southern basin of Camp Lake (Camp–Addition; where CWH was added prior to the spawning season in spring 2004), the eastern basin of Little Rock Lake (Little Rock–Control; where CWH was not manipulated), and the western basin of Little Rock Lake (Little Rock–Reduction; where CWH was removed after the 2002 spawning season). Spawning seasons occurring before or after the CWH manipulations are indicated (NA = not applicable—no manipulation for the control basin).

Variable	Camp–Addition	Little Rock–Control	Little Rock–Reduction
2002 Spawning Season			
Period relative to CWH manipulation	Before	NA	Before
Littoral CWH (logs/km)	41	344	475
Adult density (fish/ha)	27 (11–399)	49 (33–85)	64 (43–114)
Nest density (nests/km)	52.4	77.5	77.1
2003 Spawning Season			
Period relative to CWH manipulation	Before	NA	After
Littoral CWH (logs/km)	41	344	128
Adult density (fish/ha)	61 (30–306)	103 (77–152)	63 (49–84)
Nest density (nests/km)	100.0	122.5	129.0
2004 Spawning Season			
Period relative to CWH manipulation	After	NA	After
Littoral CWH (logs/km)	141	344	128
Adult density (fish/ha)	91 (54–212)	120 (93–167)	102 (78–143)
Nest density (nests/km)	87.6	76.9	62.4

to 141 logs/km (Ahrenstorff et al. 2009). Littoral CWH levels were not manipulated in the eastern basin of Little Rock Lake (Little Rock–Control; Table 1).

All three basins are relatively small, have relatively complex shorelines, and have maximum depths near 10 m (Camp–Addition: surface area = 16 ha, shoreline length = 2.9 km; Little Rock–Control: 8 ha, 1.6 km; Little Rock–Reduction: 10 ha, 2.1 km; Ahrenstorff et al. 2009). Largemouth bass are the largest piscivorous fish present in all three basins. At the start of our study, the fish community of Little Rock Lake was dominated by largemouth bass and yellow perch *Perca flavescens* and included small populations of black crappies *Pomoxis nigromaculatus*, rock bass *Ambloplites rupestris*, and central mudminnow *Umbra limi*. The yellow perch population in Little Rock–Reduction was severely depleted after the whole-basin removal of CWH in 2002 (Sass et al. 2006b). Camp Lake contains largemouth bass and bluegills *Lepomis macrochirus* as well as small populations of yellow perch and several darters *Etheostoma* spp. Avian piscivores (e.g., great blue heron *Ardea herodias*, common loon *Gavia immer*, and bald eagle *Haliaeetus leucocephalus*) are common in northern Wisconsin and have been observed at the study sites. Public fishing was prohibited on Little Rock Lake from 1984 to 2007, and Camp Lake receives minimal fishing pressure (Ahrenstorff et al. 2009). Submersed aquatic vegetation was present in each of the basins but did not dominate littoral structural habitat (Ahrenstorff et al. 2009). Macrophytes consisted primarily of short mats of isoetids, including the sevenangle pipewort *Eriocaulon aquaticum* and quillworts *Isoetes* spp. Emergent macrophytes, including watershield *Brasenia schreberi* and pond-lilies *Nuphar* spp., were found in some of the isolated bays within each basin, but all macrophytes were generally no taller than 5–10 cm at the time of largemouth bass spawning.

METHODS

Data collection.—We monitored each basin during the 2002–2004 largemouth bass spawning seasons. Largemouth bass nest sites were located visually based on the presence of eggs or larvae by using snorkel surveys that encompassed the entire shoreline of each basin to a depth of 3 m. Once located, each nest was assigned an individual site number and was labeled with a small surveyor's flag placed near the edge of the nest. The current developmental stage of the eggs (eggs, hatched fry, or free-swimming fry) was then noted. We also recorded the substrate of the nest, the presence or absence of the paternal male, and the presence of any adjacent littoral structure up to a radius of 1.25 m from the center of the nest. We used the 1.25-m cutoff to minimize the identification of structure that was not specifically incorporated into the nest in areas of dense littoral structure. Snorkel surveys were conducted in complete sweeps over a 1–2-d interval starting with the onset of spawning and were repeated at a maximum interval of 7–9 d in 2002 and 2003 and 11–12 d in 2004 (Table 2). Start dates of the surveys were

based on the onset of largemouth bass movement into the littoral zone during the prespawn period, and end dates were based on the cessation of all nesting activity. Additional research in the context of the CWH removal and addition experiments was conducted from early May to September in each year, thus decreasing the probability of missing the onset and cessation of spawning (Sass 2004; Sass et al. 2006b). It is possible that nests were missed due to the duration between snorkeling surveys, adding a degree of uncertainty to our study, particularly if the weekly distribution of nesting activity varied among basins.

Littoral CWH surveys to a depth of 2 m were conducted annually for the entire shoreline of each basin. Individual logs (diameter > 10 cm and length > 150 cm) were located visually from a boat and were recorded by using a Garmin Model 12XL Global Positioning System unit (~5-m accuracy). During each CWH survey, the entire shoreline was partitioned into adjacent 50-m transects. These transects were used as the basis for the local partitioning in our within-basin analysis. Although the entire shoreline was represented in these transects, the number and location of the transects varied annually depending on spring water levels. As detailed in previous publications (Sass et al. 2006b; Ahrenstorff et al. 2009), angling surveys conducted at least biweekly were used to estimate adult largemouth bass densities via the Chapman modification of the continuous Schnabel mark–recapture population estimation method (Ricker 1975).

Analysis.—Our analyses tested for a relationship between littoral CWH density and largemouth bass nest density at two scales: (1) within individual basins, comparing 50-m littoral transects to test for correlations between local variation in CWH density and nest density; and (2) among basins and among seasons, testing for correlations between whole-basin nest density and factors including adult largemouth bass density, littoral CWH density, and the duration of the spawning season. All statistical analyses were conducted in R software (R Development Core Team 2008).

Within each basin, we tested for a relationship between local nest density and CWH density by using linear regression ($\alpha = 0.05$). Nest density and CWH density data were $\log_e(x + 1)$ transformed, and all 50-m transects enumerated in the CWH surveys were used. The $\log_e(x + 1)$ -transformed data allowed us to detect saturating relationships, which are a potential consequence of territorial behavior in largemouth bass. Due to the possible priority effects of territorial males at this scale, we performed the within-basin analysis in two ways. First, we included all nests that were observed in a season. Second, we included only those nests that were observed during the first sweep of each survey. We recorded the specific location of each nest in the 2002 and 2003 spawning seasons, and our within-basin analysis was limited to these two seasons.

Among basins, a stepwise deletion approach based on Akaike's information criterion corrected for small sample size (AIC_c) was used to compare multiple-regression models that predicted nest density as a function of survey effort, season duration, and environmental factors (Shono 2000; Crawley

TABLE 2. Largemouth bass nest site survey information by year for three Wisconsin basins (defined in Table 1). Each survey included three to five complete sweeps of the entire littoral zone of the given basin. The maximum sweep interval (MSI) denotes the longest time interval between complete sweeps of the littoral zone via snorkel survey. Spawning seasons occurring before or after the CWH manipulations are indicated (NA = not applicable—no manipulation for the control basin).

Variable	Camp–Addition	Little Rock–Control	Little Rock–Reduction
2002 Spawning Season			
Period relative to CWH manipulation	Before	NA	Before
Survey dates	5–21 Jun	31 May–17 Jun	28 May–19 Jun
Duration (d)	16	17	22
Sweeps	3	4	4
MSI (d)	8	7	7
Nests found (total)	152	124	162
Nests found (sweep 1)	117	83	86
2003 Spawning Season			
Period relative to CWH manipulation	Before	NA	After
Survey dates	27 May–27 Jun	24 May–24 Jun	23 May–24 Jun
Duration (d)	31	31	32
Sweeps	5	5	5
MSI (d)	9	7	9
Nests found (total)	290	196	271
Nests found (sweep 1)	127	61	96
2004 Spawning Season			
Period relative to CWH manipulation	After	NA	After
Survey dates	7–28 Jun	3–23 Jun	4–24 Jun
Duration (d)	21	20	20
Sweeps	3	3	3
MSI (d)	12	11	11
Nests found (total)	254	123	131
Nests found (sweep 1)	182	57	84

2005). Specifically, we chose an initial model that predicted the full-season nest density (nests/km of shoreline) as a function of five noninteracting terms: (1) a continuous variable for the duration of the survey (d), (2) a continuous variable for the density of littoral CWH (logs/km of shoreline), (3) a continuous variable for the density of adult largemouth bass (fish/ha), (4) a discrete variable for the number of sweeps completed in the survey, and (5) a factor identifying the basin. We removed explanatory variables in a full factorial process from the initial model by using the “step” function in R, simplifying the model until we observed no decrease in AIC_c . Because of the limited number of data points ($n = 9$), the initial model ($df = 2$) included all measured explanatory variables but did not include nonlinear terms or interactions among explanatory variables. Densities of nests, adults, and CWH were \log_e transformed to account for potential saturating relationships due to male territoriality.

Rocky reefs.—Camp–Addition contained two notable rocky reefs: one large reef that extended about 75 m into the basin and was contiguous with the shoreline and one substantially smaller offshore reef. Both reefs contained very little CWH.

The large reef was surveyed every year for nests and was found to support 23 (15%) of 152 nests in 2002 and 25 (9%) of 290 nests in 2003 (nest location data for this basin are unavailable for 2004). Data on the location of individual CWH pieces (required for the within-basin analysis) were only collected for the large reef in 2003. Therefore, the large reef was excluded from the within-basin analysis of 2002 data but was included in the analysis of 2003 data. Nests were not counted on the smaller offshore reef. Based on observed nest densities for the larger rocky reef, this may have caused the total number of nests to be underestimated by about 5–20 nests at the whole-basin scale. Little Rock–Control also contained two small rocky reefs. One reef had little CWH and extended approximately 20 m off a small peninsula that was contiguous with the shoreline; this reef contained 9 (7%) of 124 nests in 2002 and 18 (9%) of 196 nests in 2003 and was included in all analyses of Little Rock–Control data. A smaller offshore reef was also present in Little Rock–Control, but nests on this reef were not counted, again resulting in underestimation of the whole-basin total by about 5–20 nests.

TABLE 3. Number of largemouth bass nests constructed within 0.5 m or within 1.25 m of littoral structure from a total of 1,703 nests observed in three Wisconsin basins, 2002–2004. Nearest structure was identified as coarse woody habitat (CWH; logs with a diameter >10 cm and a length >150 cm), boulders (>20 cm in diameter), fine woody habitat (FWH; any substantial structure made up of branches <10 cm in diameter), human-created structures (including cinderblocks and wooden planks), or structures created by North American beavers *Castor canadensis* (e.g., lodges, food caches, and runs).

Nearest structure	Within 0.5 m	Within 1.25 m
CWH	267	462
Boulder	227	306
FWH	136	210
Human structure	12	18
Beaver structure	10	15
Total nests	652	1,011

RESULTS

In total, 1,703 largemouth bass nests were observed across basins and seasons. Of those nests, 652 (38%) were constructed within 0.5 m of prominent littoral structure and 1,011 (59%) were constructed within 1.25 m of prominent littoral structure (Table 3). Nests that were within 0.5 m of structure were most commonly associated with CWH (41%; 267 of 652 nests) and large rocks and boulders (35%; 227 of 652 nests). The majority of nests (68%; 1,156 of 1,703 nests) were constructed on beds of isoetid macrophytes. Other nest substrates included sand (18%; 311 of 1,703 nests) and rocks or pebbles (6%; 108 of 1,703 nests). For those nests that were observed over the full development of larvae (eggs to swim-up fry), development lasted 6–17 d (median = 10 d).

Within-Basin Analysis

Across 50-m transects within a basin, there was weak evidence for a relationship between CWH density and whole-season largemouth bass nest density (Table 4; Figure 1). A significant ($P < 0.05$), positive saturating relationship (slope < 1.0) was observed between CWH density and nest density for Camp–Addition in 2002. Coarse woody habitat explained about 8% of the total variation in largemouth bass nest density in Camp–Addition. We observed qualitatively similar results when analyses were restricted to early season nests: a significant saturating relationship was identified and explained about 12% of the total variation for Camp–Addition in 2002 (Table 5).

Among-Basin Analysis

Among the three basins and across all three seasons, largemouth bass nest density was not well described unilaterally by basin ($r^2 = 0.05$), CWH density ($r^2 = 0.04$), or adult largemouth bass density ($r^2 = 0.14$). Survey duration ($r^2 = 0.80$, adjusted $r^2 = 0.77$, $n = 9$, $df = 7$, $F = 28.03$, $P = 0.001$; Figure 2a) and the number of complete sweeps per survey ($r^2 = 0.68$, adjusted $r^2 = 0.63$, $n = 9$, $df = 7$, $F = 14.73$, $P = 0.006$) were significant predictors of nest density, indicating that variation in spawning season duration and variation in survey effort were important to consider in our further analyses (see Table 1).

Our initial multiple-regression model including all five explanatory variables was not correlated with basin nest density ($r^2 = 0.91$, adjusted $r^2 = 0.65$, $n = 9$, $df = 2$, $F = 3.507$, $P = 0.238$, $AIC = -31.09$, $AIC_c = 80.91$). Using stepwise deletion of explanatory variables according to AIC_c values, we sequentially deleted terms for the number of sweeps, adult largemouth bass density, and the identity of the basin. Two models had

TABLE 4. Summary of linear regression analyses testing for a relationship between coarse woody habitat (CWH) density and largemouth bass nest density among 50-m transects for three Wisconsin basins (defined in Table 1). This analysis includes all nests found during the 2002 or 2003 spawning season. Seasons occurring before or after the CWH manipulations are indicated (NA = not applicable—no manipulation for the control basin).

Variable or statistic	Camp–Addition	Little Rock–Control	Little Rock–Reduction
2002 Spawning Season			
Period relative to CWH manipulation	Before	NA	Before
Slope	0.27	0.12	0.20
F	5.95	0.94	3.58
df	54	25	37
P	0.02	0.34	0.07
Adjusted r^2	0.08	0.00	0.06
2003 Spawning Season			
Period relative to CWH manipulation	Before	NA	After
Slope	0.18	0.20	0.16
F	3.18	1.61	3.57
df	56	28	39
P	0.08	0.22	0.07
Adjusted r^2	0.04	0.02	0.06

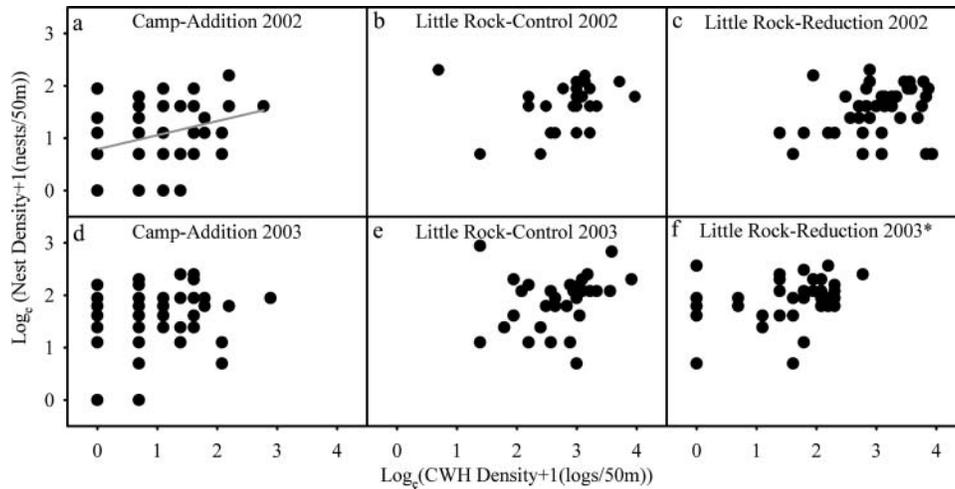


FIGURE 1. Within-basin relationships between $\log_e(x + 1)$ -transformed coarse woody habitat (CWH) density (logs/50-m shoreline transect) and $\log_e(x + 1)$ -transformed largemouth bass nest density (nests/50-m shoreline transect) for three Wisconsin basins during (a) 2002 for the southern basin of Camp Lake (Camp-Addition; where CWH was added prior to the spawning season in spring 2004; solid gray line denotes a significant relationship, $\alpha = 0.05$); (b) 2002 for the eastern basin of Little Rock Lake (Little Rock-Control; where CWH was not manipulated); (c) 2002 for the western basin of Little Rock Lake (Little Rock-Reduction; where CWH was removed after the 2002 spawning season); (d) 2003 for Camp-Addition; (e) 2003 for Little Rock-Control; and (f) 2003 for Little Rock-Reduction (asterisk indicates that the 2003 season occurred after the CWH reduction).

similarly low AIC_c values: one model included survey duration and CWH density ($r^2 = 0.88$, adjusted $r^2 = 0.84$, $n = 9$, $df = 6$, $F = 22.54$, $P < 0.002$, $AIC = -36.37$, $AIC_c = -31.57$; $\log_e[\text{nest density}] = 2.96 + 0.04[\text{survey duration}] + 0.09 \cdot \log_e[\text{CWH density}]$), and the other model included only survey duration ($r^2 = 0.80$, adjusted $r^2 = 0.77$, $n = 9$, $df = 7$, $F = 28.03$, $P = 0.001$, $AIC = -33.59$, $AIC_c = -31.59$; $\log_e[\text{nest density}] = 3.54 + 0.04[\text{survey duration}]$). Therefore, the most parsimonious model of whole-basin nest density included only

one of our measured explanatory variables (i.e., survey duration; Figure 2a) but none of our measured environmental variables. The residuals of this regression showed a positive but nonsignificant ($P = 0.086$) relationship with whole-basin CWH density (Figure 2b). Across seasons, Camp-Addition had similarly negative residual values prior to the CWH manipulation and a positive residual value after the addition, suggesting that the CWH addition exerted a positive influence on nest density (Figure 2b). Little Rock-Control had positive residual values in all 3 years.

TABLE 5. Summary of linear regression analyses testing for a relationship between coarse woody habitat (CWH) density and early season largemouth bass nest density among 50-m transects for three Wisconsin basins (defined in Table 1). This analysis includes only the nests that were found during the first sweep of the basin in each survey. Spawning seasons occurring before or after the CWH manipulations are indicated (NA = not applicable—no manipulation for the control basin).

Variable or statistic	Camp-Addition	Little Rock-Control	Little Rock-Reduction
2002 Spawning Season			
Period relative to CWH manipulation	Before	NA	Before
Slope	0.28	0.03	0.12
F	8.82	0.06	1.61
df	54	25	37
P	0.01	0.80	0.21
Adjusted r^2	0.12	-0.04	0.02
2003 Spawning Season			
Period relative to CWH manipulation	Before	NA	After
Slope	0.17	0.05	0.05
F	2.91	0.29	0.23
df	56	28	39
P	0.09	0.59	0.63
Adjusted r^2	0.03	-0.03	-0.02

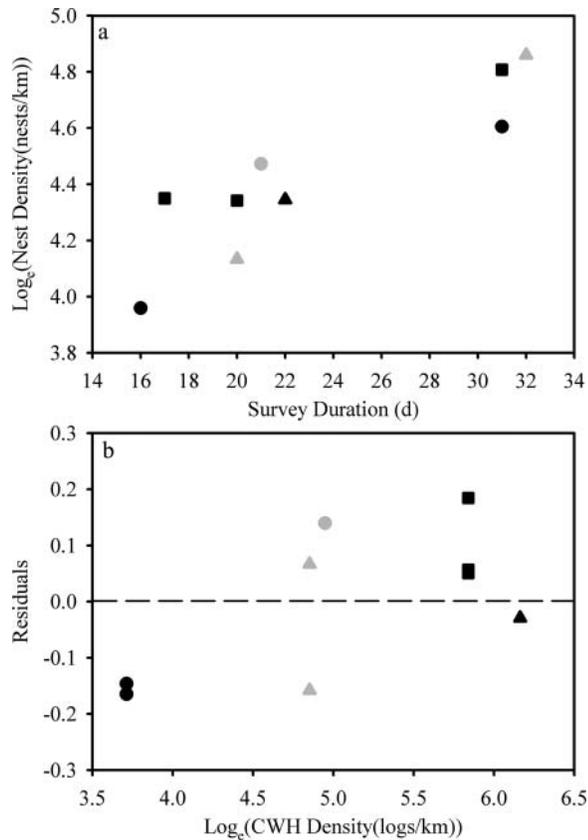


FIGURE 2. Among-basin and across-year relationships among survey duration, \log_e transformed coarse woody habitat (CWH) density (logs/km of shoreline), and \log_e transformed largemouth bass nest density (nests/km of shoreline): (a) a significant positive correlation between survey duration (comprising variation in both survey effort and nesting duration) and nest density; and (b) a positive but nonsignificant relationship between CWH density and the residuals of the regression between survey duration and nest density. The CWH manipulations and study basins are defined in Figure 1 (black symbols = spawning seasons before CWH manipulations; gray symbols = seasons after manipulations; circles = Camp-Addition; squares = Little Rock-Control; triangles = Little Rock-Reduction).

Prior to the CWH removal, Little Rock-Reduction exhibited a negative residual despite having the highest CWH density. A positive residual was observed for 2003, the season immediately after the CWH removal.

DISCUSSION

Our 3-year study provides some evidence for a positive—but seemingly weak—influence of littoral CWH density on largemouth bass nest density at the population scale. Within basins, estimates of the slope for the regression between local CWH density and nest density were consistently positive and less than 1.0 (Table 4). However, this saturating relationship was only statistically significant in one of six cases (i.e., Camp-Addition in 2002) and only explained 8% of the variance. Among nest sites, 38% were directly adjacent to some form of prominent littoral structure (i.e., were constructed within 0.5 m of struc-

ture), but a similar proportion (41%) of nests were not directly associated with structure at all (i.e., were constructed more than 1.25 m away from structure; Table 3). Among basins and across seasons, whole-basin CWH density was not included in our simplified model (Figure 2a). Rather, survey duration, which represents both spawning season duration and our survey effort, was the strongest predictor of nest density. When whole-basin CWH density was included in our regression, responses to CWH manipulation that accounted for survey duration were consistent with a positive correlation between basin CWH density and basin nest density for Camp-Addition and Little Rock-Control but not for Little Rock-Reduction (Table 1; Figure 2b).

Ultimately, the results of our study are somewhat similar to the results of previous studies of nest site selection by black basses (Vogele and Rainwater 1975; Hoff 1991; Hunt et al. 2002; Wills et al. 2004). Greater nest densities were observed in areas of abundant littoral structure than in areas of sparse structure within a basin and greater nest densities were observed after a whole-lake addition of littoral structure, but these patterns were weaker than those identified in previous studies and were often nonsignificant. We also frequently observed nest sites that were not directly associated with littoral structure or that were established in areas of sparse CWH. It is important to note that according to the stepwise deletion process, we did allow basin identity to be excluded from the two final models. Given the limited number of basins in the study, this allowed us to more directly analyze the effects of CWH density and nest density (Figure 2b) but may have confounded the influence of CWH with the influences of other basin-specific environmental variables. The weak whole-basin influence of CWH that was elucidated by this more aggressive approach is further evidence that littoral CWH did not have a strong influence on nest density in our study systems.

Overall, our study highlights the importance of littoral structure as one of many critical and interacting habitat features that drive nest site selection. For example, in the Camp-Addition and Little Rock-Control basins, rocky reefs that were largely devoid of CWH accounted for 7–15% of the nests observed and clearly provided important habitat and structure for nesting largemouth bass. Both within and outside of rocky reef habitats, the majority of largemouth bass nest sites were constructed on beds of short isoetid macrophytes. Numerous studies have noted the importance of primary substrate for black bass nest site selection and success (Wiegmann et al. 1992; Annett et al. 1996; Saunders et al. 2002; Wills et al. 2004), and several studies have indicated the importance of macrophytes as nesting substrate in systems with predominantly fine and silty substrates (Kramer and Smith 1962; Hunt et al. 2002). In our study systems, appropriate substrate may be more important than littoral structure in determining nest site selection. Littoral structure may influence local nest site selection by largemouth bass but without directly limiting the nest densities in the study systems.

Given these conclusions, several characteristics of the study systems should be considered in generalizing our findings. The

systems received little or no fishing pressure, which has been shown to negatively affect black bass nesting success (Philipp et al. 1997; Ridgway and Shuter 1997), yet it may be difficult to predict how angling pressure affects nest site selection. Many studies that report strong linkages with littoral structure were conducted in large (>40 ha) reservoirs (Vogele and Rainwater 1975; Annett et al. 1996; Hunt and Annett 2002; Wills et al. 2004), where wind and wave exposure may have stronger influences on nest site selection (Steinhart et al. 2005; Wagner et al. 2006). It is also possible that Little Rock–Control and Little Rock–Removal prior to the manipulation were saturated with CWH or largemouth bass nests, thus precluding our ability to detect patterns in nest density variation during the within-basin analyses. However, largemouth bass nest densities in the study basins were within the density ranges observed in other studies. Nest densities in our study lakes ranged from 52.4 to 129.0 nests/km, whereas Vogele and Rainwater (1975) reported 50 nests/km and Hunt and Annett (2002) reported an average of 148 nests/km. Our analysis did not consider potential within- and across-season differences in temperature and water levels. Nevertheless, due to the similar size and close proximity of our study sites, such variation should be similar across sites. Finally, there is a degree of uncertainty in our data because our sampling protocol may have been insufficient for detecting all nests, particularly unsuccessful nests or nests that developed quickly between sweeps within the survey. However, our within-basin analysis of the early season nests was qualitatively similar to the analysis that considered all nests, thus suggesting minimal bias toward littoral CWH in early season nest site selection (Table 5). Given that all surveys were conducted in complete sweeps of the entire littoral zone of each basin, we do not expect any particular bias between littoral CWH and nest site selection for the mid- and late-season nests that we may have missed.

Our study had the rare opportunity to take advantage of two controlled, whole-basin CWH manipulations and included data collected before and after the manipulations across the entire littoral zone of each basin. Over 1,700 nests were observed during the 3 years, and snorkel surveys identified each location and confirmed each spawn. In the small, northern Wisconsin study lakes, CWH did not appear to have a strong direct influence on largemouth bass nest density and site selection. However, changes in diet composition, growth rate, and foraging behavior of largemouth bass in Little Rock–Reduction (Sass et al. 2006b; Helmus and Sass 2008; Ahrenstorff et al. 2009) may generate delayed or indirect effects on nesting behavior in this system. This observation does not imply that littoral CWH is unimportant for aquatic ecosystems, and we do not recommend the removal of CWH as a management strategy.

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