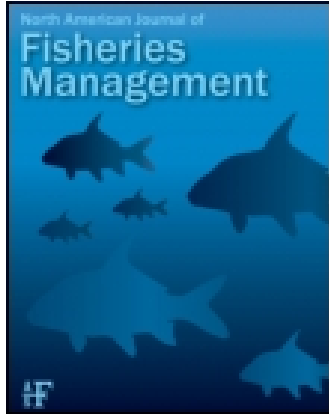


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MANAGEMENT BRIEF

Coarse Woody Habitat, Lakeshore Residential Development, and Largemouth Bass Nesting Behavior

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Abstract

Lakeshore residential development (LRD) is associated with both low riparian tree density and reduced structural complexity of the littoral zone. Fallen trees from riparian zones (coarse woody habitat [CWH]) provide littoral structure for fish refuge, substrate for invertebrate production, and habitat for nesting fish. We performed a subsurface viewing and snorkel survey comparing the spawning behavior of largemouth bass *Micropterus salmoides* in six lakes that span the known regional gradients of CWH and LRD in Wisconsin's Northern Highlands Lake District. We tested for differences in the water depth at nest sites and the nest distance to littoral structures (including every dock encountered) among lakes with contrasting CWH or LRD density. Largemouth bass nested under or near CWH in lakes with high CWH density. In lakes with low CWH, many males nested near CWH; however, nests contained smaller pieces of wood and were established in deeper water within low-CWH lakes than within high-CWH lakes. No nests were closer to a dock than to CWH, which suggested that docks do not act as surrogates for CWH. Habitat alterations associated with LRD significantly affect largemouth bass nest site location, and an understanding of these impacts will be important for maintaining viable populations of this prized game fish as LRD pressures expand.

The largemouth bass *Micropterus salmoides* is among the most economically important game fishes in North America (Department of Fisheries and Oceans Canada 1998) and supports one of the most popular recreational fisheries in the USA (Pullis and Laughland 1999). Largemouth bass can act as keystone predators in the north temperate region of the USA and can significantly alter food web interactions and community structure (Mittelbach et al. 1995). However, anthropogenic perturbations and landscape transformations associated with lakeshore residential development (LRD) can affect largemouth bass (Schuerell and Schindler 2004; Siepker et al. 2009). For example, littoral habitat alteration associated with LRD may negatively influence nesting behavior (Wagner et al. 2006; Reed and Pereira 2009).

Largemouth bass nest in lake littoral zones, where anthropogenic alterations associated with LRD can greatly reduce the amount of available nesting habitat. Changes in lake shoreline land use are associated with reductions in coarse woody habitat (CWH) through direct removal, reductions in inputs due to riparian clear-cutting, or both (Christensen et al. 1996; Jennings et al. 2003; Marburg et al. 2006). Although LRD results in the removal of various physical structures from nearshore areas, the addition of docks to the littoral zone often occurs during the development process. Docks may serve as suitable nesting habitat for largemouth bass; however, their contribution is not well studied. Understanding how largemouth bass respond to habitat changes associated with LRD has become more salient with increased shoreline development over the last few decades.

Natural littoral zone structures such as CWH serve as critical habitat for various aspects of the largemouth bass nesting process. For nesting males, large pieces of wood provide protection from avian predation (Helfman 1981; Hunt et al. 2002) and possibly refuge from larger aquatic predators, such as northern pike *Esox lucius* or muskellunge *E. masquinongy*. Coarse woody habitat also provides a physical substrate for egg attachment (Hunt et al. 2002), protects eggs from photodegradation (Coble 1975; Miller 1975), and reduces egg damage from wave action (Miller and Kramer 1971). After hatching occurs, CWH provides larvae with immediate refuge from brood predators (Annett et al. 1996). Indeed, many studies have shown that male largemouth bass exhibit a strong affinity for these protective structural features in nest site selection (Kramer and Smith 1962; Miller 1975; Annett et al. 1996; Hunt et al. 2002).

Although previous research has investigated how largemouth bass nesting behavior relates to LRD and physical structures separately, to our knowledge no study has addressed these variables simultaneously. We investigated whether largemouth bass nesting behavior varied in lakes across gradients in both CWH

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density and LRD density. We also assessed the role of docks as surrogates for CWH in providing nesting habitat. We expected largemouth bass to nest in proximity to CWH when possible and to nest near other (i.e., natural) littoral structures in lakes with low CWH densities. We also expected that largemouth bass would establish their nests at deeper locations in lakes with lower CWH densities to compensate for the lack of littoral structure. Finally, we did not expect largemouth bass to use docks as a nesting habitat surrogate for CWH.

METHODS

Largemouth bass nests were observed during late May to mid-June 2009 in six lakes within Wisconsin's Northern Highlands Lake District. These six lakes are at the extreme ends of the observed regional gradients in CWH and LRD densities (Figure 1; Table 1; North Temperate Lakes Long-Term Ecological Research Program database, lter.limnology.wisc.edu). Study lakes were chosen primarily based on CWH and LRD densities, and two lakes were selected to represent each of three lake categories: high CWH–low LRD; low CWH–low LRD; and low CWH–high LRD. Lakes were also selected to have relatively similar surface area, water clarity, and species composition. We hypothesized that largemouth bass nesting behavior could be influenced by the presence of large predators; we therefore selected lakes where muskellunge, northern pike, or both were common (Wisconsin Department of Natural Resources 2005). These species were observed in each lake during our sampling.

Active nest locations were viewed in the littoral zone by an observer wearing polarized sunglasses in a boat propelled by a trolling motor (Wagner et al. 2006) and by a snorkeler swimming alongside the boat (Bozek et al. 2002; Saunders et al. 2002; Suski and Philipp 2004). Sampling began at the boat landing and proceeded counterclockwise around the shoreline until 30 nests or the entire lake was surveyed. Physical characteristics of occupied nests, including water depth and horizontal distance to physical structures within 5 m (CWH, sub-CWH [defined below], and docks), were measured. We considered an occupied nest to be any nest that was actively guarded by a male large-

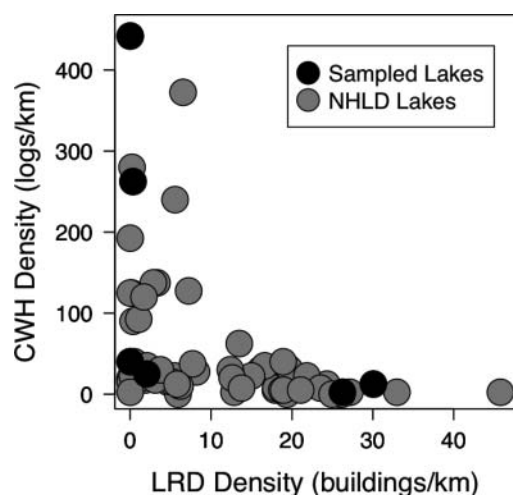


FIGURE 1. Relationship between lakeshore residential development (LRD) and coarse woody habitat (CWH) for 62 lakes within Wisconsin's Northern Highlands Lake District (NHLD; black shaded circles = study lakes; gray shaded circles = previously sampled NHLD lakes). Data were obtained from Christensen et al. (1996; CWH > 5 cm in diameter) and from the North Temperate Lakes Long-Term Ecological Research Program database (CWH > 15 cm in diameter).

mouth bass. Coarse woody habitat was defined as any piece of wood that was 10 cm or greater in diameter and 150 cm or greater in length. Sub-CWH was classified as any piece of wood that was less than 10 cm in diameter or less than 150 cm in length; sub-CWH was noted only if its distance from the nest was 0 m. Every dock encountered was snorkel-surveyed for occupied nests. Docks were defined as structures that extended at least 1.5 m from shore and were situated in water that was 0.25 m or deeper at the structure's deepest point.

A 3×3 chi-square contingency table was constructed to test for differences in nest distance from CWH (0, <1, or >1 m) among the three CWH–LRD lake categories (Sokal and Rohlf 1995). Another 3×3 chi-square contingency table was constructed to test for differences in nest distance to different types of wood (0 m to CWH, 0 m to sub-CWH, or >0 m to any wood type) among the CWH–LRD lake categories. Water depth at

TABLE 1. Study lake characteristics, including lake category (based on densities of coarse woody habitat [CWH] and lakeshore residential development [LRD]), lake area, CWH and LRD densities, number of largemouth bass nests sampled, and number of docks sampled, in Wisconsin's Northern Highlands Lake District. Data for Bay Lake was obtained from Christensen et al. (1996; CWH > 5 cm in diameter); all other data were obtained from the North Temperate Lakes Long-Term Ecological Research Program database (CWH > 15 cm in diameter).

Lake	CWH/LRD lake category	Area (ha)	CWH density (pieces/km)	LRD density (buildings/km)	Nests sampled	Docks sampled
Bay	High/low	69.0	442.0	0.0	30	0
Indian	High/low	29.1	262.5	0.4	11	1
Allequash	Low/low	165.3	55.0	0.0	11	0
Little John	Low/low	63.4	27.5	2.1	27	5
Brandy	Low/high	45.1	12.5	30.1	12	49
Johnson	Low/high	34.7	0.0	26.2	17	54

nest locations (square-root transformed to meet normality assumptions) was compared between CWH–LRD categories by using an analysis of variance and Tukey's post hoc honestly significant difference comparison. Water depth at nest sites was also compared between the two lakes within each CWH–LRD category by using Student's *t*-tests. Normality assumptions were confirmed by use of the Shapiro–Wilk test. All statistical analyses were conducted in R software (R Development Core Team 2010).

RESULTS

Nest distance from CWH differed significantly among the CWH–LRD lake categories ($\chi^2 = 26.45$, $df = 4$, $P < 0.0001$; Figure 2A). Over 95% of occupied nests were within 1 m of CWH when CWH was readily available (i.e., the high CWH–low LRD category: median absolute deviation = 0). When CWH density was low (low CWH–low LRD and low CWH–high LRD categories), over 40% of occupied nests in both categories were within 1 m of CWH (median absolute deviation = 0.62 and 0.00, respectively; Figure 2A).

When all types of wood (i.e., CWH and sub-CWH) were taken into consideration, the type of wood that was nested on or under varied among CWH–LRD lake categories ($\chi^2 = 38.04$, $df = 4$, $P < 0.0001$; Figure 2B). In lakes where CWH was readily available, occupied nests were almost exclusively located near CWH. However, sub-CWH was used in nest construction when CWH densities were low: the percentage of occupied nests that incorporated sub-CWH was 39% for the low CWH–low LRD category and 58% for the low CWH–high LRD category (Figure 2B). In all lake categories, over 80% of all largemouth bass nests were observed directly on or under wood of some type (Figure 2B). Regardless of lake category, over 70% of all sampled nests were within 1 m of CWH and over 90% of all nests were within 1 m of some type of wood (Figure 2C). However, only one nest (i.e., <1% of the total number of nests surveyed) was observed within 1 m of a dock and that nest was closer to CWH than to the dock (Figure 2C).

Nests in the high CWH–low LRD category were located at significantly shallower water depths than nests in the two low-CWH categories regardless of LRD density (analysis of variance: $F = 17.93$, $df = 2$, $P < 0.0001$; Tukey's post hoc honestly significant difference test: low CWH–high LRD versus high CWH–low LRD, $P < 0.0001$; low CWH–low LRD versus high CWH–low LRD, $P < 0.0001$; low CWH–low LRD versus low CWH–high LRD, $P = 0.99$; Figure 3). Furthermore, within each lake category, the nests in the deepest water were located directly on or under CWH. Average water depth at nest sites did not vary between the two lakes within each category (*t*-test: high CWH–low LRD, $P = 0.62$; low CWH–low LRD, $P = 0.35$; low CWH–high LRD, $P = 0.60$).

DISCUSSION

Largemouth bass associate with physical structures during the nesting process (Annett et al. 1996). Other studies have

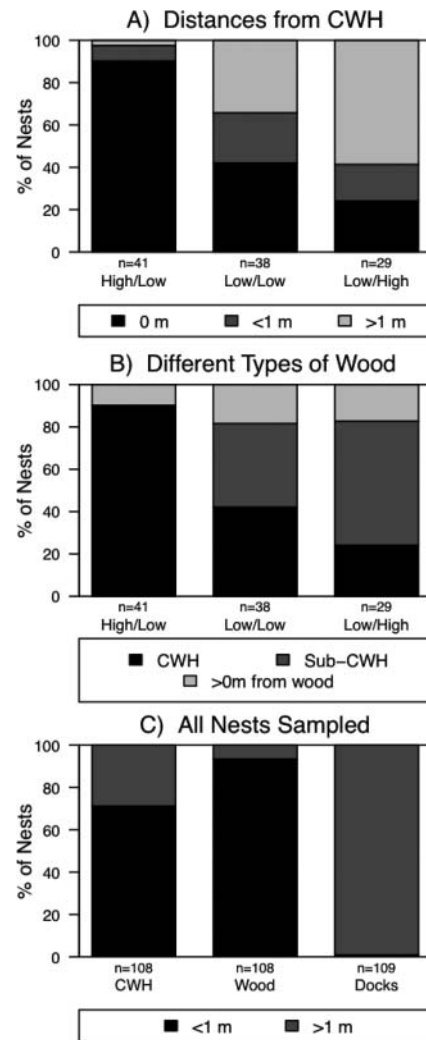


FIGURE 2. Percentage of largemouth bass nests observed across different littoral habitats: (A) nests located at varying distances from coarse woody habitat (CWH; 0, <1, or >1 m) in three lake categories (denoted by CWH density and lakeshore residential development [LRD] density, respectively: high/low, low/low, and low/high; nest distance to CWH was significantly different among lake categories: χ^2 , $P < 0.001$); (B) nests that were directly on or under CWH, directly on or under sub-CWH, or not directly on or under any type of wood structure (nest distance to different types of wood was significantly different among lake categories: χ^2 , $P < 0.001$); and (C) nests (regardless of lake category) located within 1 m of or more than 1 m from; CWH, any type of wood (CWH and sub-CWH; only nests on or under sub-CWH were considered for that wood type), or a dock (n = total number of nests sampled).

shown differences in largemouth bass nesting behavior between lakes with high and low densities of LRD (Wagner et al. 2006; Reed and Pereira 2009), although the mechanisms driving these trends have not been determined. Our results show that effects of LRD on largemouth bass nesting behavior are related to CWH. We found that largemouth bass used larger pieces of wood (CWH) when such pieces were available; otherwise, they established nests on or under smaller pieces of wood (sub-CWH). Furthermore, we conclude that docks do not act as surrogates

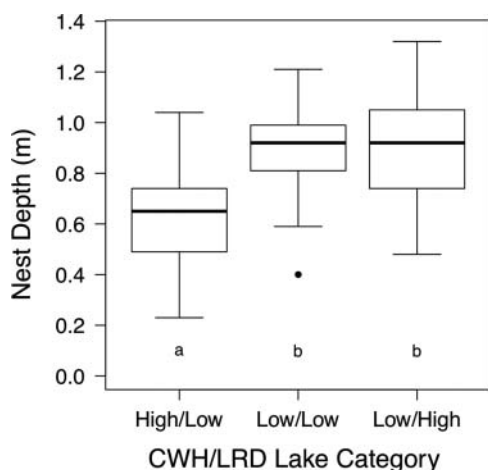


FIGURE 3. Box-and-whisker plots of water depth at largemouth bass nest sites across three lake categories (defined in Table 1; line within box = median; ends of box = first and third quartiles; ends of whiskers = 1.5 times the interquartile range; filled circle = outlier). Depth at nest sites was significantly different among the lake categories (analysis of variance: $F = 17.93$, $df = 2$, $P < 0.001$). Values with the same lowercase letter were not significantly different (Tukey's post hoc honestly significant difference test: $P < 0.001$).

for CWH because none of the observed nests were closer to a dock than to CWH. Although LRD is associated with altered littoral zone habitats (Christensen et al. 1996), our results suggest that the water depth at nest locations is driven directly by CWH density rather than by the level of LRD.

We found that largemouth bass showed a high affinity toward nest sites that included some type of woody habitat. Males almost exclusively nested adjacent to CWH when CWH was abundant, and surprisingly we observed that many still nested near CWH even when the CWH density was low. Although CWH seemed to be a preferred nesting habitat, CWH was not always accessible. In lakes with low CWH density, male largemouth bass incorporated smaller pieces of wood or sub-CWH into their nests. As over 90% of all nests were located within 1 m of CWH or directly on or under sub-CWH, our results suggest that all types of wood, regardless of size, could serve as potential nesting habitat for largemouth bass.

In the Northern Highlands Lake District, CWH naturally varies in density (Figure 1); however, CWH is always low when LRD density exceeds 9 buildings/km (Marburg et al. 2006). Although lakes with high LRD densities contain fewer natural nesting habitats for largemouth bass, anthropogenic structures such as docks are often associated with LRD. However, our results indicate that docks do not provide suitable nesting habitat for largemouth bass. Although an investigation of factors that might deter males from nesting near docks was beyond the scope of this study, while sampling the high-LRD lakes we observed landowners on or near docks and engaging in activities such as swimming, boating, playing with dogs, and angling. Such activities could discourage largemouth bass from nesting

near docks. Factors driving this relationship should be explored further.

For all CWH–LRD categories, the nests in the deepest water were observed directly on or under CWH, suggesting that largemouth bass nest in deeper locations to incorporate CWH in nest construction. These findings support the hypothesis that largemouth bass effectively seek out specific critical habitat characteristics despite the relative abundances of those characteristics in high-LRD lakes (Wagner et al. 2006). Our research also offers an explanation for why largemouth bass position their nests in deeper areas within developed lakes. Future studies should examine how these differences in nesting behavior relate to nest success.

In conclusion, anthropogenic processes, such as CWH removal associated with LRD, alter largemouth bass spawning behavior and nest site location. The addition of docks to lake littoral zones does not compensate for the removal of natural woody habitat. Our findings illustrate the need for management policies to conserve natural littoral habitat in highly developed lakes. Lake managers should also consider augmentation of natural nearshore spawning habitat in systems with both elevated and increasing LRD densities. Although CWH was apparently a preferred nesting habitat for largemouth bass, we found that all sizes and shapes of wood were important for nesting when CWH occurred at low densities. Future studies should look at lakes in these CWH–LRD categories or along a CWH–LRD gradient to analyze nest success in these different environments. An understanding of largemouth bass nesting behavior will be important for maintaining viable populations of this prized game fish as LRD pressures expand.

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