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Habitat Selection of Nesting Smallmouth Bass *Micropterus dolomieu* in Two North Temperate Lakes

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Abstract.—Anthropogenic disturbances in nearshore littoral zones of lakes may affect spawning habitat and recruitment of smallmouth bass *Micropterus dolomieu*, yet habitat models that quantify habitat selection by smallmouth bass in lakes are not well developed nor are their limitations understood. In this study we quantified smallmouth bass spawning habitat in two northern Wisconsin lakes and developed resource selection functions to describe habitat selection of spawning sites. In general, nest sites in both lakes were located near wood or rock cover, at water depths of 0.5–3.0 m, and contained nest substrates where at least 40 percent of the particles were 6.4–149.0 mm in diameter. However, specific habitat selection by smallmouth bass differed between lakes. The best resource selection function for Big Crooked Lake contained six significant habitat variables (i.e., sand, gravel, cobble, embeddedness, rock cover, and wood cover) and correctly classified eighty-four percent of the nest sites in Big Crooked Lake. The best resource selection function for Sanford Lake contained four significant habitat variables (i.e., sand, gravel, average embeddedness, and rock cover) and correctly classified ninety-two percent of the nest sites in Sanford Lake. Despite high success of within-lake classification of nest sites in both lakes, generality of models differed substantially when tested between lakes for validation. The best models developed in Big Crooked Lake in 1997 and 1998 correctly classified only 25 and 8 percent of the nests in Sanford Lake for respective years, whereas the best model developed in Sanford Lake in 1997 and 1998 correctly classified 67 and 100 percent of the nests in Big Crooked Lake. The less complex model developed in Sanford Lake was more transferable between lakes, correctly predicting nest sites over a wider range of habitat types. Understanding limitations of habitat selection is critical for development of habitat models to aid protection and restoration of littoral zone habitats.

Introduction

In Wisconsin, smallmouth bass *Micropterus dolomieu* are less abundant today than they were historically (Becker 1976; Lyons 1991). In streams, declines in distribution and abundance are believed to result from habitat destruction, dumping of industrial and domestic sewage, poor land use such as overpasturing and improper tillaging, and over exploitation (Schneberger 1972; Becker 1976; Lyons 1991). In lakes, trends have been less clear due to a lack of research focus, but widespread alterations to riparian areas and littoral zone habitats by riparian area development have influenced the distribution and abundance of smallmouth bass and other intolerant, lake-resident fishes (Jennings et al. 1996; Jennings et al. 1999). Among other things, effects of development on littoral zones include reductions in large woody structure (Christensen et al. 1996; Jennings et al. 1996) and modified substrates and shoreline slopes (Jennings et al. 1996) often used by smallmouth bass for spawning (Hoff 1991).

Because littoral zone habitat likely influences smallmouth bass recruitment (Serns 1984; Hoff 1991), a quantitative understanding of fish-habitat relations is necessary to assess consequences of changes in habitat quality and quantity on fish populations. Despite the importance of habitat, few models exist that accurately quantify spawning habitat use or selection by smallmouth bass and other fishes in lakes. Habitat models have been used to describe general habitat use of smallmouth bass (Schneberger 1972; Coble 1975; Lukas and Orth 1995), predict standing stocks and production of fish (Fausch et al. 1988; Lyons 1991; Sowa and Rabeni 1995), and mitigate perturbations to aquatic environments (U.S. Fish and Wildlife Service 1980; Schamberger et al. 1982; Edwards et al. 1983). Habitat use and selection models have been key components of stream habitat restoration/protection strategies based on techniques such as Habitat Evaluation Procedures (HEP) and the Instream Flow Incremental Methodology (IFIM) (Stalnaker 1979; U.S. Fish and Wildlife Service 1980; Schamberger et al. 1982; Beecher et al. 1993), and application of these models in lakes may provide a useful tool to help manage lake habitats.

Theoretically, habitat selection models broadly reflect habitat quality, as fish select habitats that optimize fitness (i.e., reproductive potential) (Boyce and McDonald 1999). Critical to developing and using habitat selection models is the creation of models that not only accurately reflect use of the highest quality habitat, but also are transferable across a wide variety of aquatic environments. But because habitats are highly variable within and among lakes, quantification of optimal habitats by fish is complicated, particularly when proportions of key habitat features are limited or absent (Arthur et al. 1996; Boyce and McDonald 1999). In theory, habitat models based on habitat selection rather than just habitat use are recommended because they attempt to account for differences in resource availability (Manly et al. 1997) which makes them more transferable across aquatic systems. However, the degree to which they actually are transferable is largely untested.

In north temperate lakes, habitat use by smallmouth bass may differ substantially across an array of lakes that vary considerably in morphological features such as littoral zone area, shoreline slope, substrate composition, macrophyte structure, and the amount of large woody structure (Schupp 1992; Emmons et al. 1999). Because many fishes in north temperate lakes spawn in littoral zones (Becker 1983), evaluating spawning habitat use and selection in lakes with differing littoral zone characteristics is important for their management. In lakes, high intensity of effort is required to collect habitat use and availability data needed for developing selection models, and the use of specialized sampling gear is often necessary (i.e., S.C.U.B.A.). For this reason, habitat selection models for fish have not yet been extensively developed and tested in lakes. The objective of this study was to quantify habitat selection of spawning smallmouth bass in two lakes with different littoral zone habitat characteristics and assess the generality of the habitat selection models developed across both lakes.

Methods

Study Site

Big Crooked and Sanford lakes are located on the property of Dairymen's, Inc., a privately owned resort near Boulder Junction, Wisconsin. Big Crooked Lake is a drainage lake with an area of 276 hectares, 8.1 km of shoreline, and a maximum depth of 11.6 m. The lake is oligotrophic with low alkalinity and is very clear. The littoral zone is composed of three physiographic regions: a larger shallow sand flat encompassing the entire north, east and southwest shorelines, a steep rocky cobble area located along the west shoreline, and a sand and silty bay area along the southern shoreline. Rocks and boulders, deposited from the last glaciation, occur infrequently in all but the larger, shallow sand flat areas of the lake, and large woody structure is uncommon in the littoral zone. The lake is undeveloped except for a small, private resort on the north end of the lake, and access is restricted to members only. Harvest is restricted to catch and release angling only for smallmouth bass. The main fish species occurring in Big Crooked Lake include: walleye *Stizostedion vitreum*, muskellunge *Esox masquinongy*, northern pike *Esox lucius*, smallmouth bass, yellow perch *Perca flavescens*, rock bass *Ambloplites rupestris*, mimic shiners *Notropis volucellus*, and white suckers *Catostomus commersoni*.

Sanford Lake is located on the northern end of Dairymen's, Inc. property and has an area of 35.6 ha, 3.9 km of shoreline, and a maximum depth of 15.5 m. Sanford Lake is a mesotrophic drainage lake and is stained with tannic acid. The shoreline is undeveloped except for one boat landing and a small picnic area. Harvest is restricted to catch and release angling only for smallmouth bass. Trees fall into the lake providing abundant large woody structure throughout the littoral zone; rocks and boulders are uncommon. The main fish species in Sanford Lake include: muskellunge, smallmouth bass, walleye, yellow perch, rock bass, white suckers, bluegill *Lepomis macrochirus*, pumpkinseed *Lepomis gibbosus*, and golden shiner *Notropis crysoleucas*.

Approach

Resource selection functions (RSF) for smallmouth bass nest sites were developed by quantifying habitat at nest sites and random points in the littoral zone of the two lakes. Logistic regression was used to develop the RSF's as it is the preferred analysis for differentiating between two classes of response variables (i.e., presence or absence) (Prager and Fabrizio 1990; Manly et al. 1997). Logistic regression uses the function:

$$\pi = \frac{e^u}{1+e^u}$$

where:
π = the probability of a smallmouth bass nest
e = the inverse natural logarithm of 1
$u = k + m_1x_1 + m_2x_2 + \ldots + m_ix_j$
k = the regression constant
m_i = the regression coefficients
x_j the values of the independent variables

The −2 log likelihood statistic was used to test significance of each resource selection function. This statistic measures the deviation of observed values from the resource selection function and is analogous to residual sum-of-squares in linear regression (Hosmer and Lemeshow 1989). Chi-square analyses were used to test the significance of individual regression coefficients in each function with alpha set at P less than or equal to 0.05. All habitat variables were used in simple logistic models to determine the probability of nest site selection; correct classification rates were then evaluated for each significant model. Habitat variables were then selected for input into multiple logistic regression analyses based on their performance in the univariate logistic models, examination of Pearson correlation matrix coefficients, and their biological relevance. Coefficients of all habitat variables where P is less than or equal to 0.20 were entered into the multiple logistic regression analysis; all others were removed from consideration to help ensure residual explanatory power was not masked by colinearity (Hosmer and Lemeshow 1989). As each new variable was added to the model, it was sequentially compared to the previous model using the G-score and the Akaike information criteria that assessed the increase in model fit (Linhart and Zucchini 1986; Hosmer and Lemeshow 1989). Based on model significance and correct classification rates, the best one, two, three, four, five, and six habitat variable models were developed (when possible) for each lake and year. In addition, the five best models for each lake and year, based on correct classification rates for predicting nest sites, were also developed. To assess model generality (i.e., transferability between lakes) the best resource selection function (i.e., those models having the best correct classification rates) from each lake was tested in the other lake using the habitat availability data from that lake to assess how well that model predicted the relative probability of nest site selection.

Quantifying Used Habitat

To locate smallmouth bass nests, the entire littoral region of each lake was surveyed by snorkeling or scuba every other day during the spawning season. Nests were located using three methods: a boat was motored along the littoral zone region of the lakes and nests were visually detected using Polaroid glasses; divers snorkeled/dove or were towed through deeper areas of littoral zones; and scuba gear was used to dive along the deepest edges of littoral zones and underwater reefs. Once located, each nest was marked with numbered flags and the date recorded indicating when the nest became inhabited, when eggs were deposited, and when fry emerged from the nest.

After fry emerged from each nest, nest habitat was quantified. Variables measured at each nest included distance from shore, water depth, nest concavity, nest diameter, substrate sizes, small woody structure (wood < 0.04 m diameter), substrate embeddedness, cover type, orientation, size, and distance of cover from the edge of each nest, and bottom slope. Percentages of each particle size were visually estimated using a 1296 cm^2 enumeration grid composed of 36, 6 cm × 6 cm grid squares. Water depth, distance to shore, and distances to cover (i.e., large woody structure and rocks) were measured with a tape from the edge (i.e., rim) of the nest. Nest diameter was the mean of two perpendicular transects measured by stretching a tape from nest edge to nest edge. Nest concavity quantified how deep the nest was excavated into the bottom substrates and was measured with a tape from a plastic rod laid across the nest, rim-to-rim, to the bottom of the nest. Slope was calculated by dividing the difference between two depth measurements (rise) by the nest diameter (run). Depths for slopes were measured at the two points where a transect tape intersected the nest rim; the transect tape was laid perpendicular to shore across the nest.

Quantifying Available Habitat

Habitat characteristics of each lake's littoral zone were collected using 100 randomly placed transects along the perimeter of each shoreline. Random transect locations were selected based on elapsed time traveled from an arbitrary start location on the shore. A mean elapsed time to idle the survey boat around the entire lake along the 2 m contour was calculated and individual transects were placed at the 100 randomly drawn times. A maximum depth of 3.0 m was used because smallmouth bass did not nest at depths greater than 3.0 m in either Big Crooked or Sanford lakes. Habitat variables were collected along each transect using a 1 m^2 quadrat at points located every two meters from shore until a depth of 3.0 m using snorkel and scuba equipment. The same variables used to quantify habitat in nests were also quantified at each transect point. Distances to cover were measured from each transect point to each cover item. Slope was calculated as the difference in two depths (rise) collected at the transect points immediately before and after the sample point divided by that distance (run).

Results

Available Habitat

Overall, littoral zone habitat differed substantially between lakes (Figure 1). Big Crooked Lake had extensive areas of shallow, flat, bottom contours as evidenced by the large number of transect points needed to quantify habitat in the littoral zone to the 3.0 m depth contour. Sanford Lake on the other hand, had steeper littoral zone slopes. Distributions of substrate particle sizes were significantly different between Big Crooked and Sanford lakes (Kolmogorov-Smirnov Two Sample Test, $K = 0.113$, $P \leq 0.001$). In Big Crooked Lake, 76.8 percent of the littoral zone was covered by sand, 10.0 percent by silt and 7.6 percent by gravel. Coarse organic debris, cobble, rubble, small boulders, and large boulders made up the remainder of the littoral zone substrates with percentages of less than three percent each. In contrast, 70.0 percent of the littoral zone in Sanford Lake was covered by silt, 12.7 percent sand, and 4.4 percent coarse organic debris. Gravel, cobble, rubble, small boulders, and large boulders comprised the remainder of the littoral zone with percentages of less than three percent each. While present in limited numbers in Big Crooked Lake, larger rocks (i.e., rubble, small boulders, large boulders) used for cover in littoral zones were more common in Sanford Lake. And because Sanford Lake has a smaller surface area, the density of larger rocks used for cover was also proportionally greater than in Big Crooked Lake. Larger substrates were found at the lake margins of both lakes (0–3 m from shore) whereas finer substrates occurred in deeper water. In both lakes, silt was positively related to depth, whereas sand was negatively related to depth. Occurrence of gravel peaked between 1.5 and 2.0 m in depth. Cobble, rubble, small boulders, and larger boulders occurred throughout the range of depths sampled.

The occurrence of large woody structure was low and more evenly distributed across all depth ranges sampled in Big Crooked Lake whereas in Sanford Lake, large woody structure was more abundant. In fact, despite its smaller size, Sanford Lake had nearly twice the amount of large woody structure than Big Crooked Lake. Moreover, a greater proportion of wood in Sanford Lake was found at shallower depths whereas wood was more evenly distributed with depth in Big Crooked. Small woody structure ($\leq$ 0.04 m diameter) was abundant throughout all depth ranges in both Big Crooked and Sanford lakes, but it was more abundant in Sanford Lake.

Habitat Use and Selection

In Big Crooked Lake in 1997, the proportion of substrates found in smallmouth bass nests sites were primarily gravel (78.3%) and cobble (18.5%) with smaller amounts of sand (1.7%) and rubble (1.5%). Similar proportions of substrate were used in 1998; gravel (77.5%) and cobble (18.7%) were most common, and sand (2.9%) and rubble (0.9%) were less common. In Sanford Lake, the distribution of substrate sizes in nests was smaller. In 1997, the proportion of substrates found in smallmouth bass nests were sand (20.6%), gravel (57.7%), cobble

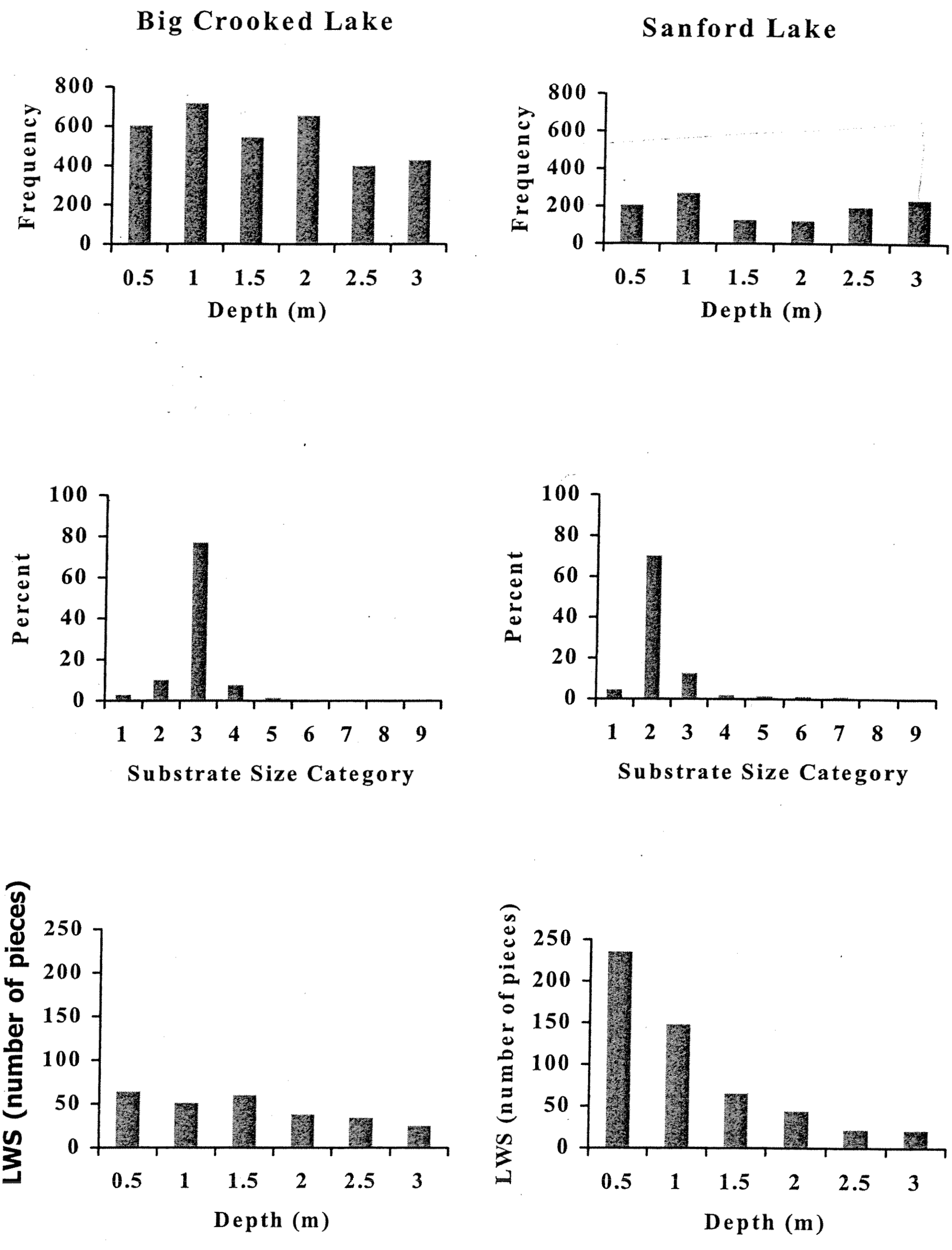

Figure 1. Distributions of habitat features in the littoral zones of Big Crooked and Sanford lakes, Wisconsin. Water depths represent the number of equidistant transect points that occurred at depths less than 3.0 m collected from 100 random transects placed in the littoral zones of each study lake. Substrate size categories are 1 = coarse organic debris, 2 = silt (< 0.2 mm), 3 = sand (0.2–6.4 mm), 4 = gravel (6.5–76.0 mm), 5 = cobble (76.1–149.9 mm), 6 = rubble (150.0–303.9 mm), 7 = small boulder (304–609.9 mm), 8 = large boulder (> 610.0 mm), 9 = bedrock. Large woody structure (LWS) represents the distribution of pieces of large woody structure (15 cm diameter and >1.0 m long) relative to littoral zone depth increments.

(23.8%), and rubble (0.8%). In 1998, substrates were similar, composed of silt (2.8%), sand (28.1%), gravel (63.2%), cobble (5.7%), and rubble (0.1%). The greatest between-lake difference in spawning sites was that the amount of gravel present in the substrate matrix was significantly higher in Big Crooked Lake than Sanford Lake in 1997–1998 (Mann–Whitney Rank Sum, $P < 0.05$). Proportions of cobble and rubble used in nests were not significantly different between lakes in 1997 nor 1998 (Mann–Whitney Rank Sum, $P > 0.05$).

Smallmouth bass usually selected areas having coarser substrates and cover proximal to the nest location relative to its availability in both lakes. The best resource selection functions developed in Big Crooked Lake contained four to six variables, whereas in Sanford Lake resource selection functions had four or less habitat variables.

Big Crooked Lake 1997

Rock cover was the single best univariate predictor of smallmouth bass nests in 1997, with a correct classification rate of 13 percent (Table 1). Gravel (6.4–76.0 mm) and cobble (76.1–149.9 mm) substrate produced the best two-variable resource selection function with a correct classification rate of 27 percent. The variables gravel substrate, cobble substrate, and rock cover produced the best three variable resource selection function with a correct classification rate of 44 percent. The best overall model was a four variable resource selection function containing the habitat variables sand, gravel, nest rock cover, and wood cover with a correct classification rate of 61 percent (Table 2). While a significant resource selection function containing five habitat variables was produced, the correct classification rate for nests declined to 56 percent. In addition to the best models produced, various combinations of sand, gravel, cobble, substrate embeddedness, wood cover, rock cover and depth consistently produced models that correctly predicted nest sites in Big Crooked Lake for 1997. All models reliably predicted nest absence.

Sanford Lake 1997

The percentage of gravel substrate was the single best univariate predictor of smallmouth bass nests in 1997 with a correct classification rate of 58 percent (Table 1). A combination of gravel substrate and nest rock cover produced the best bivariate re-

Table 1. The best univariate, bivariate, and trivariate resource selection functions predicting smallmouth bass spawning sites in Big Crooked and Sanford lakes during 1997, Vilas County, Wisconsin. Number of nests and random plots for Big Crooked were 24 and 3,338, and for Sanford Lake were 27 and 1,139, respectively. Models and all variables in each model are significant at $P < 0.05$.

Variables in model	Regression coefficient	Constant	−2 Log likelihood	McFadden Rho	P	Classification rates Presence (%)	Classification rates Absence (%)
			Big Crooked Lake 1997				
Embeddedness	−1.115	−1.626	74.104	0.260	<0.001	6	99
Gravel	0.070	−7.787	120.647	0.423	<0.001	12	99
Rock cover	1.079	−9.463	84.408	0.296	<0.001	13	99
Gravel Cobble	0.199 0.197	−20.593	166.969	0.586	<0.001	27	99
Gravel Cobble Rock cover	0.193 0.187 0.805	−24.191	182.124	0.639	<0.001	44	99
			Sanford Lake 1997				
Wood cover	13.037	−5.125	67.072	0.287	<0.001	19	99
Cobble	0.111	−4.652	67.222	0.288	<0.001	27	99
Gravel	0.113	−5.179	141.391	0.605	<0.001	58	99
Gravel Wood cover	0.113 14.503	−7.528	174.212	0.745	<0.001	70	99
Gravel Cobble Wood cover	0.112 0.103 18.888	−9.566	17.71	0.846	<0.001	81	99

source selection function with a correct classification rate of 70 percent. Gravel, rubble, and nest wood cover comprised the best three-variable resource selection function with a correct classification rate of 81 percent. A combination of gravel and rubble substrates with nest rock cover and wood cover produced the best four variable resource selection function with a correct classification rate of 86 percent (Table 2). Other models predicting nest sites with greater than 75 percent accuracy used various combinations of the variables of sand, gravel, rubble, substrate embeddedness, nest wood cover, nest rock cover, and water depth.

Big Crooked Lake 1998

In Big Crooked Lake in 1998, the habitat variable rock cover was again the single best predictor of nest sites with a correct classification rate of 31 percent (Table 3). Gravel substrate (6.4–76.0 mm) was the second best single predictor of nest sites with a

Table 2. The five best resource selection functions predicting smallmouth bass nest presence or absence in Big Crooked and Sanford lakes, Vilas County, Wisconsin for 1997. Number of nests and random plots for Big Crooked were 24 and 3,338, and for Sanford Lake were 27 and 1,139, respectively.

Variables in model	Regression coefficient	Constant	−2 Log likelihood	McFadden Rho	*P*	Classification rates Presence (%)	Classification rates Absence (%)
Big Crooked Lake 1997							
Gravel	0.206	−28.49	209.799	0.736	<0.001	61	99
Cobble	0.188						
Rock cover	1.330						
Wood cover	19.102						
Sand	−0.164	−16.64	202.419	0.710	<0.001	56	99
Gravel	0.093						
Cobble × embeddedness	0.023						
Rock cover	1.238						
Wood cover	22.857						
Sand	−0.244	−15.259	200.285	0.703	<0.001	52	99
Gravel	0.081						
Sand × gravel	0.007						
Rock cover	1.238						
Wood cover	24.487						
Sand	−0.185	−12.863	194.926	0.684	<0.001	50	99
Gravel	0.066						
Rock cover	1.060						
Wood cover	21.762						
Gravel	0.114	−16.986	193.093	0.677	<0.001	48	99
Cobble × depth	0.040						
Embeddedness	−0.765						
Rock cover	1.166						
Wood cover	14.255						
Sanford Lake 1997							
Gravel	0.141	−7.636	207.563	0.888	<0.001	86	99
Cobble	0.170						
Rock cover	−1.106						
Wood cover	20.465						
Sand	0.075	−13.963	202.528	0.866	<0.001	82	99
Gravel	0.158						
Rubble	0.156						
Wood cover × embeddedness	4.511						
Gravel	0.112	−0.566	197.71	0.846	<0.001	81	99
Cobble	0.103						
Wood cover	18.888						
Gravel	0.104	−6.558	181.346	0.776	<0.001	78	99
Cobble × wood cover	1.532						

correct classification rate of 17 percent, and substrate embeddedness was the third best single variable predictor of nest sites with a correct classification rate of 13 percent. The best two-variable model used rock cover and percent gravel substrate to correctly classify 51 percent of nests. The best three-variable model used rock cover, percent gravel substrate, and substrate embeddedness to correctly classify 60 percent of nests. Our best resource selection function for predicting nest sites in Big Crooked Lake in 1998 contained six habitat variables: sand, gravel, cobble, substrate embeddedness, rock cover, and wood cover (Table 4). This resource selection function correctly classified 84 percent of the nests in Big Crooked Lake (Table 4). The second best resource selection function included the variables sand, gravel, substrate embeddedness, rock cover, and wood cover with a correct classification rate of 78 percent. The third best resource selection function included the variables sand, cobble, rock cover, and an interaction term, gravel-rock cover and had a correct classification rate of 73 percent. Other models predicting nest sites with greater than 70 percent accuracy used various combinations of the variables sand, gravel, cobble, substrate embeddedness, wood cover, and rock cover.

Sanford Lake 1998

In Sanford Lake in 1998, the habitat variable gravel substrate was the single best predictor of nest sites with a correct classification of 73 percent (Table 3). Substrate embeddedness was the second best single predictor of nest sites with a correct classification rate of 26 percent. Gravel substrate and rock cover produced the best bivariate resource selection function with a correct classification rate of 85 percent. Sand and gravel substrate and rock cover produced the best three-variable resource selection function with a correct classification rate of 87 percent. The best resource selection function for predicting nest sites in Sanford Lake in 1998 contained the habitat variables sand, gravel, substrate embeddedness, and nest rock cover with a correct classification rate was 92 percent (Table 4). The second best resource selection function predicting smallmouth bass nests included the variables gravel, substrate embeddedness, rock cover, and wood cover with a correct classification rate of 89 percent.

Across Lake Validation

The best resource selection functions developed on both lakes for both years accurately predicted nest sites within the lakes from which they were developed. However, the best model developed in Big

Table 3. The best univariate, bivariate, and trivariate resource selection functions predicting smallmouth bass spawning sites in Big Crooked and Sanford lakes during 1998, Vilas County, Wisconsin. Number of nests and random plots for Big Crooked were 38 and 3,338, and for Sanford Lake were 51 and 1,139, respectively. Models and all variables in each model are significant at $P < 0.05$.

Variables in model	Regression coefficient	Constant	−2 Log likelihood	McFadden Rho	P	Classification rates Presence (%)	Absence (%)
Big Crooked Lake 1998							
Rock cover	1.468	−11.259	205.711	0.494	<0.001	31	99
Gravel	0.069	−7.251	189.781	0.444	<0.001	17	99
Embeddedness	−1.316	−0.878	159.497	0.383	<0.001	13	99
Gravel Rock cover	0.088 1.662	−18.048	282.397	0.687	<0.001	51	99
Gravel Embeddedness Rock cover	0.080 1.264 1.346	−13.403	307.081	0.814	<0.001	60	99
Sanford Lake 1998							
Gravel	0.120	−5.416	299.068	0.710	<0.001	73	99
Embeddedness	−2.693	6.593	127.639	0.305	<0.001	26	97
Gravel Rock cover	0.143 −1.148	−3.082	342.887	0.814	<0.001	85	99
Sand Gravel Rock cover	0.050 0.148 −1.023	−5.233	362.124	0.860	<0.001	87	99

Table 4. The five best resource selection functions predicting smallmouth bass nest presence or absence in Big Crooked and Sanford lakes, Vilas County, Wisconsin for 1998. Number of nests and random plots for Big Crooked were 24 and 3,338, and for Sanford Lake were 24 and 1,139, respectively. Models and all variables in models are significant at P < 0.05.

Variables in model	Regression coefficient	Constant	−2 Log likelihood	McFadden Rho	*P*	Classification rates Presence (%)	Classification rates Absence (%)
Big Crooked Lake 1998							
Sand	0.535	−75.474	367.390	0.882	<0.001	84	99
Gravel	0.553						
Cobble	0.517						
Rock cover	4.295						
Embeddedness	−2.124						
Wood cover	13.921						
Sand	0.146	−24.971	348.010	0.835	<0.001	78	99
Gravel	0.119						
Embeddedness	−1.000						
Rock cover	2.035						
Wood cover	17.865						
Sand	0.168	−17.49	339.372	0.815	<0.001	73	99
Gravel × rock cover	0.037						
Cobble	0.171						
Embeddedness	−2.047						
Gravel	0.120	-20.674	331.592	0.796	<0.001	71	99
Gravel × cobble	0.002						
Embeddedness	−1.030						
Rock cover	1.688						
Gravel	0.141	−25.32	323.062	0.776	<0.001	70	99
Gravel × cobble	0.003						
Rock cover	1.801						
Sanford Lake 1998							
Sand	0.058	10.034	377.379	0.896	<0.001	92	99
Gravel	0.141						
Embeddedness	−3.906						
Rock cover	−1.342						
Gravel	0.121	9.003	365.497	0.873	<0.001	89	99
Embeddedness	−3.408						
Rock cover	−1.068						
Wood cover	10.373						
Sand	0.050	−5.233	362.124	0.860	<0.001	87	99
Gravel	0.148						
Rock cover	−1.023						
Gravel	0.140	-4.552	352.031	0.836	<0.001	86	99
Rock cover	−0.919						
Wood cover	11.053						
Sand	0.052	−9.342	343.126	0.815	<0.001	80	99
Gravel	0.138						
Wood cover	11.765						
Gravel × cobble	0.003						
Rock cover	1.801						

Crooked Lake poorly predicted nest sites in Sanford Lake, whereas, the best model developed in Sanford Lake was more transferable to Big Crooked Lake (Table 5). The best within-lake model developed in Big Crooked Lake during 1997 included the habitat variables gravel, cobble, rock cover, and wood cover and had a correct classification rate of 61 percent in Big Crooked Lake (Table 4). However, when this model was applied to Sanford Lake (1997), it produced a correct classification rate of only 25 percent. Likewise, the best model for Big Crooked Lake 1998 included the habitat variables sand, gravel, cobble, substrate embeddedness, rock cover, and wood cover and had a correct classification rate of 84 percent. When applied to Sanford Lake (1998), it only produced a correct classification rate of 8 percent.

The Sanford Lake models were more general when applied to Big Crooked Lake. The best model for Sanford Lake in 1997 included the habitat variables gravel, rubble, rock cover, and wood cover, and this model had a correct classification rate of 86 percent. When applied to Big Crooked Lake (1997), it produced a correct classification rate of 67 percent of nests. Similarly, the best model for Sanford Lake 1998 included the habitat variables sand, gravel, substrate embeddedness, and rock cover and had a correct classification rate of 92 percent. Use of this model in Big Crooked Lake (1998) produced a correct classification rate of 100 percent of nests. In all models, nest absence was predicted well.

Discussion

While research has shown how specific habitat changes may affect fish community structure (Jennings et al. 1996, 1999), it has not yet clearly demonstrated how these habitat changes affect fish populations. Quantitative habitat models, such as resource selection functions, are prerequisite to understanding and predicting consequences of habitat changes in littoral zones of lakes. Previous studies suggest smallmouth bass prefer cool, clear, deep bodies of water with rocky substrate on which to construct nests (Latta 1963; Mraz 1964; Coble 1975; Becker 1983). However, past work in lakes has focused mainly on general habitat features and have not accounted for microhabitat features of nest sites, nor how heterogeneous littoral zone habitats influence habitat use within and across lakes. For instance, Neves (1975) generalized smallmouth bass nest habitat as scooped-out areas of coarse gravel and fist-sized rubble in South Branch Lake, Maine, but did not look at littoral zone habitat availability nor the distribution pattern of nests relative to distributions of sites having suitable habitat. In contrast, Rejwan et al. (1999) acknowledged that heterogeneous patterns of shoreline influenced

Table 5. Across-lake validation for the best resource selection functions developed for Big Crooked and Sanford lakes in 1997–1998 and their correct classification rates for model predictions.

Variables in model	Year	Model source	Model application	McFadden Rho	Classification rates Presence (%)	Absence (%)
Gravel Cobble Rock cover Wood cover	1997	Big Crooked Big Crooked	Big Crooked Sanford	0.736	61 25	99 100
Sand Gravel Cobble Embeddedness Rock cover Wood cover	1998	Big Crooked Big Crooked	Big Crooked Sanford	0.882	84 8	99 100
Gravel Rubble Rock cover Wood cover	1997	Sanford Sanford	Sanford Big Crooked	0.888	86 67	99 97
Sand Gravel Embeddedness Rock cover	1998	Sanford Sanford	Sanford Big Crooked	0.896	92 100	99 82

smallmouth bass nest placement linking water temperature, shoreline sinuosity, bottom rugosity, and fetch with smallmouth bass nest sites. However, that study did not detail habitat at the nest scale, nor did it integrate the availability of habitat in the littoral zone.

In our study, we developed resource selection functions for spawning smallmouth bass by quantifying used and available habitat within the littoral zone of two north temperate lakes. Our research uncovered two trends. First, smallmouth bass clearly select specific habitat features of littoral zones where multiple habitat features combine to produce suitable spawning habitat conditions for bass. In both lakes, as habitat variables were added to the models, correct classification rates of nest sites increased. Yet in contrast, classification rates of sites where nests were absent were universally high among models, lakes, and years. The best models developed in Big Crooked Lake were six-variable models whereas those in Sanford Lake were four-variable models that contained similar base variables: substrate size and cover. Most models that incorporated interaction terms were not significant or had lower correct classification rates than models without interaction terms.

A second trend revealed that gravel, cobble, and wood cover were important in the best models produced for both lakes in both years. Gravel substrate was the most consistent variable in most multiple logistic regression models even though it was less abundant in Sanford Lake than in Big Crooked Lake. Greater than 40 percent gravel in a 1 m^2 area dramatically increased the probability of a smallmouth bass nest occurring and cobble substrates also were important. Coarse substrates likely increase survival of eggs by reducing development of fungus and helping keep eggs oxygenated (Eipper 1975); these are the habitat features of smallmouth bass nests identified by other researchers. Our findings clearly showed that gravel and cobble substrates are requisites for nest site construction.

Variables associated with nest protection increased the probability of predicting nest presence. Previous studies had documented and described smallmouth bass nesting in gravel and cobble substrates, and near boulders, fish cribs and other types of cover (Beeman 1924; Hubbs and Bailey 1938; Mraz 1964). Wood cover, which bass use for nest protection, can increase survival of swim-up fry (Hoff 1991). Wood cover was more abundant in Sanford Lake than in Big Crooked Lake, yet was clearly important in both. Because smallmouth bass protect nests, the presence of cover, such as wood, likely reduces the nest perimeter that males must defend.

Rock cover however, differed in selection models among lakes. In Big Crooked Lake, rock cover was positively related to the presence of bass nests while in Sanford it was negatively related to bass nests. This may simply result from differences in the distribution of rock cover in lakes relative to other important nest attributes. In Big Crooked Lake, large boulders were associated with suitable quantities of gravel, which seemed to be prerequisite for nest site selection by smallmouth bass. The placement of fish cribs and logs near coarse substrates in Big Crooked Lake offered additional cover for nesting male smallmouth bass, whereas those placed in silt and sand areas were not used. In Sanford Lake, many rocks and boulders were found in silt and sand substrates common throughout the lake, which bass avoided. Habitat selection by bass appears to be hierarchical with juxtaposition of individual habitat characteristics being important. For example, without suitable substrate, sites with cover were not selected by bass.

Water depth was not a significant habitat variable in resource selection functions developed in Big Crooked and Sanford lakes, yet depth clearly is important. Nests were found at depths from 0.1 to 3.0 m. Smallmouth bass have previously been reported to construct nests at depths up to 6.5 m (Mraz 1964). In Big Crooked and Sanford lakes, no suitable habitat occurs at these depths because substrates there are primarily silt. Because we restricted data collection from 0 to 3.0 m depths, the depth variable does not appear to be important, but this is an artifact of our restricted scale of sampling. From our observations, water depths of 1–3 m define suitable habitat which likely affect recruitment and survival of young smallmouth bass in these lakes. Habitat models for smallmouth bass need to integrate depth along with other physical habitat features identified in the resource selection functions.

Nest site selection did not appear to be dependent on nest distance to shore. However, nest sites in Big Crooked Lake were located farther from shore than nest sites in Sanford Lake and from our observations, nests located closer to shore were destroyed more frequently by wave surges. As data collection and research continues, distance from shore may become a significant variable in models. A model that identifies the quality of spawning sites relative to fitness that maximizes survival could greatly improve management of smallmouth bass.

We originally attempted to develop resource selection functions for each of the three geomorphically distinct habitat regions in Big Crooked Lake but this was not possible. Smallmouth bass did not select spawning sites in the wide, flat region of the basin that is composed primarily of sand substrate, nor in the large, silty region that occurs behind a series of islands and underwater humps. However, nest distributional patterns between lakes provided insights about habitat selection. Spatial patterns of nests clearly reflected the general distribution of habitat in lakes. These findings reflect those of Rejwan et al. (1999) who found that smallmouth bass nest sites were aggregated around specific lake habitat features of lakes. In Big Crooked Lake, nests were clumped in the region of the lake where combinations of coarse substrate and suitable cover occurred. Smallmouth bass hierarchically selected habitat: first they chose general lake areas with suitable habitat, then at a microhabitat scale, they select specific nest locations. In contrast, nests in Sanford Lake are distributed throughout the basin because there appears to be no observable differences in the distribution of spawning substrates as well as less coarse substrate overall.

Although resource selection functions described habitat selection by smallmouth bass in both lakes, the quality of those habitats are only inferred as a function of used versus available habitat features specific to each lake (i.e., relative probability of use). In this study, both lakes have "optimal habitat" defining a local optimal condition as calculated by the logistic function, because habitats differ considerably between lakes. Determining which of the two lakes has better habitat is a current limitation of resource selection functions. A solution is to develop site-specific models for each system (sensu DeGraaf and Bain 1986). Under these circumstances, models for lakes containing lower quality habitat (i.e., lower survival of eggs and fry) can still have "optimal habitat" defined within the constraints of that system as they represent the best available habitats. Developed in this context, these models have a reduced ability to be transferred across systems. In addition to problems associated with differences in overall availability of habitat that clearly differed between these two lakes, density dependent factors (Fretwell 1972) can affect habitat selection that can compound transferability problems (Bult et al. 1999). For instance, in 1998 a larger portion of the bass population spawned in both lakes and some nests sites were reused from 1997 in both Big Crooked and Sanford lakes. In both years, habitat did not appear to be limiting in Big Crooked Lake and thus most spawning males occupied a narrow range of "optimal" site conditions. However in Sanford Lake, where the density of spawning smallmouth bass is much greater and gravel/cobble substrates are more limited, we observed greater variation in spawning habitat used as bass moved into sites having smaller substrate sizes.

Resource selection functions developed in Big Crooked and Sanford lakes in 1997 and 1998 performed well, correctly predicting nest sites within the lake from which they were developed. However, the resource selection functions developed in both lakes in 1997 had fewer significant habitat variables and lower within-lake correct classification rates than the resource selection functions developed in 1998. This may have been due to low sample sizes in 1997, with just 24 nest sites encountered in Big Crooked Lake. This small sample of nest sites with low habitat diversity led to the development of resource selection functions that were more general and incorporated less significant habitat variables than models developed in 1998. But while correct classification rates were lower within lakes, across lake correct classification rates were higher during validation.

How population size and size structure affect model development is unclear, but may have had a bearing in this study. In addition to being less abundant, males that spawned in 1997 were larger than the males in 1998 and these larger fish had selected the "optimal sites"; suboptimal sites were not used in this year in either lake. These optimal sites had large amounts of gravel, cobble, and large rock for nest protection, which could be found in both Big Crooked and Sanford lakes. This may have allowed for greater transferability of the resource selection functions in 1997. It has been reported that younger, smaller smallmouth bass males do not spawn every year (Ridgway 1991), and that time of spawning may be affected by degree-days accumulated before spawning occurs. In the spring 1997, ice-out was late in northern Wisconsin. The first nests were started during the first week of June and continued for approximately three weeks. This may account for the low number of spawning males and nest sites that year.

Until recently, resource selection functions have been used primarily in terrestrial environments and rivers (Martin 1985; Erickson et al. 1998; Millspaugh et al. 1998; Beecher et al. 1993), largely due to the amount time and effort required to collect available habitat data in lakes. Rejwan et al. (1999) found that smallmouth bass nest sites were aggregated around specific habitat features within littoral areas of lakes (protected bays with exposed gravel substrates and suitable nesting cover). Because nests sites have been documented as being fragile and sensitive to change during the first few weeks of occupation (Eipper 1975; Shuter et al. 1980), they should be protected from both direct (littoral zone modifications) and indirect (watershed and riparian modifications) anthropogenic disturbances. The resource selection functions developed in our study will allow resource managers to identify the most critical spawning habitat in lakes even with suboptimal habitat. Once this critical habitat is identified, steps can be taken to protect such areas so that spawning habitat is not degraded, which may limit survival of young-of-year bass and affect overall recruitment to adults (MacLean et al. 1981).

Smallmouth bass spawning populations fluctuate from year to year. Smallmouth bass presence/absence in streams has been linked to the amount of gravel substrate and cover present (Lyons 1991). In our study, nearshore lake areas that had greater than 40 percent coarse substrate were selected for nest placement. More information is needed regarding used and unused habitats within lakes so we can identify critical spawning habitats across a greater range of lake habitat conditions. Resource selection functions have not been widely applied to lacustrine environments, and our work provides an initial step in this direction. Increased use of resource selection functions could help biologists maintain or increase populations that show stress due to habitat loss or over-exploitation. Ultimately, this tool will provide criteria for evaluating shoreline development and help formulate guidelines for habitat protection, mitigation, and restoration of littoral zones of north temperate lakes.

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