Can Habitat Alteration and Spring Angling Explain Largemouth Bass Nest Success?

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Abstract.—Largemouth bass *Micropterus salmoides* nest in shallow littoral areas, making them vulnerable to negative effects of habitat alteration due to development of lake shorelines and fishing during the spring nesting period. For instance, alteration of shorelines may reduce the quality and abundance of nesting habitat, and the high visibility of nests and the aggressive guarding behavior of nesting males increase their vulnerability to fishing. In 2004, we monitored nest distribution and success and quantified local nest habitat features, lakewide angler effort, and lakeshore development patterns in five Michigan lakes to determine the extent to which habitat alteration and fishing limit the number of nests that produce swim-up fry. Lakes spanned a range of lakeshore dwelling densities (8–22 dwellings/km), allowing us to determine the extent to which nest success varies within and among lakes due to local (e.g., substrate and cover) and lakewide (e.g., dwellings/km and fishing effort) factors. Surprisingly, local habitat characteristics were not important determinants of the probability that a nest would produce swim-up fry ($P > 0.05$). At the whole-lake scale, however, nest success was negatively related to dwelling density; the probability of producing swim-up fry declined from 0.77 in the lake with the lowest dwelling density to 0.45 in the lake with the highest dwelling density ($P = 0.018$). Lakewide estimates of angling effort could not explain the difference among lakes, indicating the likely importance of quantifying angling at finer spatial scales. Knowledge of the magnitude of anthropogenic effects and the spatial scale at which they operate is integral for the management of black bass *Micropterus* spp.

As keystone predators and valued sport fish in North American lakes, black basses *Micropterus* spp. (specifically largemouth bass *M. salmoides* and smallmouth bass *M. dolomieu*) possess life history characteristics that make them vulnerable to perturbations associated with human development of lake shorelines. These species spawn in the spring, when water temperatures are near or above 15°C. Males construct nests in the substrate of relatively shallow littoral areas, often in close proximity to physical structure (Annett et al. 1996; Hunt and Annett 2002; Wills et al. 2004). After attracting and mating with a female, the male black bass guards the eggs and developing fry until the brood disperses (Ridgway 1988; Ongarato and Snucins 1993; Philipp et al. 1997). This period of parental care by male black bass may last more than a month (Brown 1984), during which time the males are highly active and guard offspring aggressively while feeding only opportunistically (Ridgway 1988; Hinch and Collins 1991).

Events occurring during these early life stages are important for first-year recruitment of black bass

(Ludsin and DeVries 1997). Therefore, an understanding of anthropogenic factors affecting the early life history of black basses is necessary to further our knowledge of their biology and to effectively manage them. Nest success, often defined as the occurrence of a nest that produces swim-up fry (Philipp et al. 1997), is considered to be an important event in the recruitment process and may affect the abundance of age-0 black bass that will ultimately survive to the first winter (Ridgway and Shuter 1997). Although compensatory mortality may occur, neither the magnitude of the effect on nesting success nor the capacity of black bass populations to compensate is fully understood.

Because black bass typically nest in shallow littoral areas, human development of lake shorelines (i.e., lakeshore dwelling density) and associated activities may negatively affect nesting success in two ways. First, removal of structure (i.e., rooted vegetation or coarse woody material) and alteration of littoral substrate may increase the risk of predation and/or siltation (Christensen et al. 1996; Radomski and Goeman 2001; Jennings et al. 2003). For instance, Hunt and Annett (2002) concluded that male largemouth bass selected nest building sites near physical structure (e.g., woody debris) in preference to habitats that lacked structure; their results suggested that removal of structure through activities such as lakeshore development (LD) alters largemouth bass nest distributions and ultimately negatively affects nest

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success. Second, the high visibility of black bass nests and the aggressive guarding behavior of nesting males increase their vulnerability to angling (Ridgway 1988). Removal of male black bass from the nest even for short periods of time reduces the male's ability to guard the nest, which ultimately increases predation risk on black bass eggs and larvae and increases the likelihood that the male will prematurely abandon the nest, thereby negatively affecting production of successful nests (Philipp et al. 1997; Ridgway and Shuter 1997; Suski et al. 2003).

Most studies of nesting black bass have been conducted in ponds or on a single lake or reservoir, and such studies often focus on smallmouth bass (but see Philipp et al. 1997). Therefore, a paucity of information exists on the potential impacts and relative importance of LD (and associated habitat modification) and angling for patterns of nest distribution and nesting success of largemouth bass within and across lakes. Furthermore, because most previous studies of factors affecting nesting success have only been performed at one spatial scale—that of the local nest—it is unclear whether these assorted factors operate at the local nest scale (i.e., through factors measured at the nest scale, such as the depth of the nest), a lakewide scale (i.e., through factors measured at the lake scale, such as lake productivity), or both. The goals of this study were to determine whether largemouth bass nest success varies with both local and lakewide features and to explore the relative importance of habitat modification versus spring angling to patterns of nest success. To accomplish these goals, we conducted a study examining largemouth bass reproductive success at multiple spatial scales in six southeastern Michigan lakes with a wide range of lakeshore dwelling densities (8–22 dwellings/km). Our primary objective was to determine the extent to which local- and lakewide-scale residential LD and habitat variables and lakewide angling pressure affect the probability of successful largemouth bass nest production. As a secondary objective, we sought to gain further insight into our nest success findings by evaluating the spatial distribution of largemouth bass nests relative to natural and anthropogenic lakeshore habitat characteristics. We also highlight the use of generalized linear mixed models (GLMMs), which have properties that make them useful in the analysis of fisheries data (Venables and Dichmont 2004) but which have not been widely applied in fisheries to date.

Methods

Study Area

We monitored six lakes located in Washtenaw and Livingston counties in southeastern Michigan during May and June 2004 to assess the importance of local nest- and lakewide-scale habitat characteristics to largemouth bass reproductive success (Figure 1). We selected lakes that were similar morphometrically but that spanned a wide range of lakeshore dwelling densities from 7.8 to 22.3 dwellings/km (Table 1). All lakes were mesotrophic, stratified, and accessible to public fishing.

Lake Characteristics

We viewed nest success as a function of lakewide and local characteristics. We included three whole-lake features: lakeshore dwelling density (lakewide LD), angler effort, and total phosphorus (TP; Table 2). Lakeshore dwelling density was determined based on visual observations by boat to quantify the number of riparian dwellings within 50 m of each lake; we then divided the number of dwellings by the lake perimeter (km). We sampled for TP by use of integrated epilimnetic water samples collected with a tube sampler during the month of July. The TP was measured by persulfate digestion (Menzel and Corwin 1965) followed by standard colorimetry (Murphy and Riley 1962). We determined angler effort separately for May and June by conducting two instantaneous angler counts per week in each lake (once per randomly chosen week day and weekend day). We randomly selected (without replacement) time of day (morning, mid-day, or evening) for each survey, and surveyed lakes in haphazard order. During each survey, we visually assessed fishing activity for all boats on the lake from the vantage of a boat using binoculars. We recorded the number of anglers per boat, the location of the boat (near the shoreline or open water), and the gear type used when possible. Following Philipp et al. (1997), we recorded an angler as potentially targeting black bass if he/she was using tactics (fishing near the shoreline and employing appropriate lures or jigs) that could potentially catch nesting black bass. We followed the methods of Lockwood et al. (1999) to expand each survey count to an estimate of the total number of angler-hours using the equation

$$\hat{E}_{pdj} = F_p A_{dj}, \tag{1}$$

where $\hat{E}$ = estimated angler-hours, F = the number of fishable hours during the entire period, p = day type (e.g., weekends or weekdays during May or June), A = number of anglers, d = day, and j = count. We calculated two estimates of lakewide angling effort (total h/km of shoreline): one for all anglers and one that included only those anglers that potentially targeted nesting black bass. We generated separate estimates for 8–28 May and 29 May–27 June because it is illegal to target or harvest black bass in Michigan lakes prior to the Saturday of Memorial Day weekend (29 May in 2004). Within each month, we averaged weekend estimates and also weekday estimates and
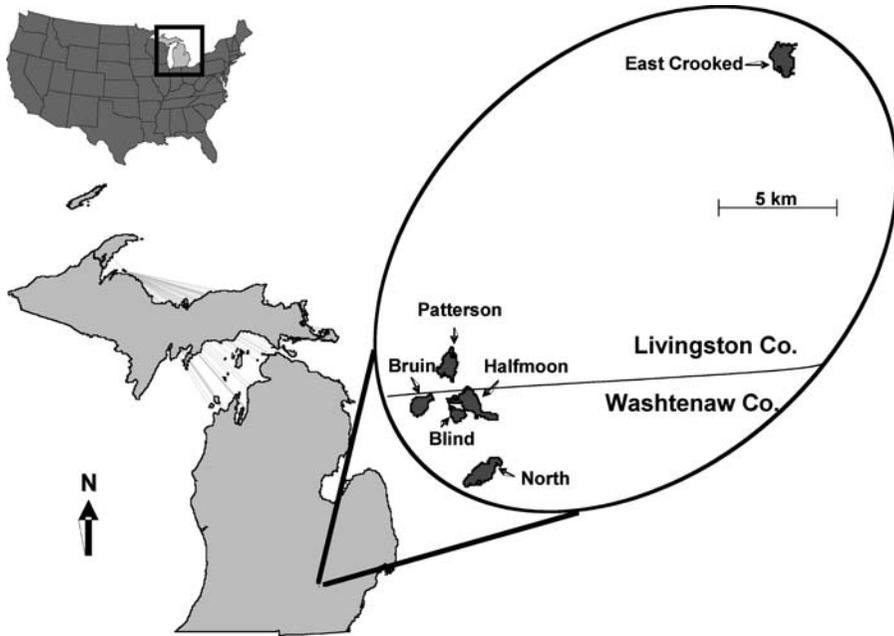
FIGURE 1.—Location of the six Michigan study lakes surveyed for an assessment of largemouth bass reproductive success.

then summed those means to generate the final estimates for each month. We calculated variance separately for weekend and weekday estimates (as per equation 58 in Lockwood et al. 1999) and then summed the two values.

Nest Location and Reproductive Success

We surveyed the littoral area for largemouth bass nests using boats powered by electric trolling motors. We conducted surveys at least biweekly for new nests and to examine the status of previously located nests. Once a new nest was located, we marked it with a numbered marker and recorded its location with a differentiated Global Positioning System (GPS; Trimble GeoExplorer). After marking the nest, we used an aquascope or snorkeling to observe local nest characteristics (see below) and the presence or absence of a male largemouth bass, eggs, larvae, and/or fry. We

considered a nest to be successful if fry were observed actively swimming above the nest (Philipp et al. 1997).

Nest Characteristics

Once a nest was located, we recorded the dominant substrate type (e.g., silt, sand, etc.) and the presence of cover (boulders, woody debris, macrophytes) within a 1-m radius of the nest, along with the depth of the nest. We also recorded the development type of the nearest shoreline (local LD type) as either undeveloped, developed–maintained (developed but with no retaining wall; e.g., a shoreline with a maintained lawn), or developed–retained (a shoreline with riprap or a retaining wall). Using the GPS locations, we calculated distance to shore. Also, we determined wind exposure for each nest from existing geographical information system (GIS) coverages. We classified each nest as having high or low wind exposure based

TABLE 1.—Lake morphometry and water quality characteristics for six Michigan study lakes surveyed for largemouth bass reproductive success. Shoreline complexity is defined as the ratio of the length of the shoreline to the circumference of a circle with an area equal to that of the lake.

Lake	Dwelling density (dwellings/km)	Lake area (ha)	Mean depth (m)	Total P (μg/L)	Shoreline complexity
Bruin	7.8	52.7	3.74	15.3	1.20
Blind	9.5	28.8	4.05	12.5	1.32
East Crooked	14.6	100.5	3.97	19.9	1.84
Halfmoon	17.7	97.4	6.77	13.1	2.12
North	21.5	90.5	3.53	16.6	1.67
Patterson	22.3	64.1	5.58	22.0	1.79

on the nest's location in relation to the prevailing southwest winds (Table 2). In addition, we used the existing GIS coverages to quantify the total amount of spawning habitat with regard to local LD type and wind exposure.

Statistical Analyses

Nest success.—We omitted nests from our analysis if their fate could not be determined. We only included predictor variables in our analysis if we had mechanistic hypotheses regarding their likely effects on largemouth bass nest success. We recognized two general mechanisms through which local habitat features and angling pressure could affect nest success. First, habitat features may directly affect nest success through physical and chemical constraints on egg survival. Second, local habitat features and angling pressure in combination may indirectly influence the vulnerability of nests to failure through parental male abandonment and nest predation. Two additional factors that potentially affect nest success must also be factored into the analysis. First, nest site features not subject to anthropogenic alteration may influence nest success. Second, attributes at the whole-lake scale may affect the average probability of nest success for a given lake.

We used a GLMM to determine whether local nest site characteristics or whole-lake characteristics affected the probability that a largemouth bass nest would successfully produce swim-up fry (Table 2). Generalized linear mixed models are extensions of generalized linear models (GLMs) and include random effects. Fixed-effects models (e.g., GLMs) assume that all observations are independent of each other; thus, these models are not appropriate for analysis of hierarchical or correlated data structures (see Wagner et al. 2006). In our analysis, GLMMs were used to accommodate dependence among observations within lakes and to accommodate the hierarchical nature of the data (e.g., largemouth bass nests nested within lakes). Both GLMs and GLMMs are extensions of the general linear model and allow response variables to follow any probability distribution in the exponential family

(e.g., normal, binomial, and Poisson). Generalized linear mixed models are composed of three model components, including (1) a linear predictor that is a linear combination of regression coefficients, (2) a link function that relates the mean of the response data to the linear predictor, and (3) a response distribution from the exponential family of distributions. For a more-detailed overview of the theory and use of GLMs and GLMMs in fisheries research, see Venables and Dichmont (2004).

To begin, we built separate models of nest success as a function of each covariate that was hypothesized to affect nest success. After significant uncorrelated predictors were identified, we then included them in a single model. The model can be described as a two-level model; the first level models the probability of a nest succeeding as a function of local nest characteristics, and the second level models the average probability of nest success for each lake as a function of lake characteristics. The probability of success was assumed to follow a Bernoulli distribution. The response variable (Y_{ij}) is binary, equaling 1 if nest i in lake j was successful and 0 if nest i in lake j failed. The probability of success of nest i in lake j is defined as $\phi_{ij} = \Pr(Y_{ij} = 1)$. The general form of the two-level model is as follows:

Level 1:

$$\eta_{ij} = \beta_{0j} + \sum_{q=1}^{Q} \beta_{qj} X_{qij}, \qquad (2)$$

where η_{ij} is the log odds of success for nest i in lake j (i.e., the level 1 link function [logit link], $\eta_{ij} = \log[\phi_{ij}/(1 - \phi_{ij})]$, β_{0j} is the mean log odds of success for lake j; and β_{qj} is the effect of covariate X_{qij} on the log odds of success ($q = 1$ to Q, where Q is the total number of level 1 covariates).

Level 2:

$$\beta_{0j} = \gamma_{00} + \sum_{s=1}^{S} \gamma_{sj} W_{sj} + u_{0j},$$

$$\beta_{1j} = \gamma_{10}, \ldots, \beta_{qj} = \gamma_{q0}, \qquad (3)$$

TABLE 2.—List of covariates used in a generalized linear mixed model analysis of largemouth bass nest success in Michigan lakes. Level 1 covariates are those measured at the nest scale; level 2 covariates are those measured at the lake scale.

Level 1 covariates	Level 2 covariates
Dominant substrate type	Lakeshore development (dwellings/km)
Presence/absence of cover (boulders, woody debris, macrophytes)	Angler effort (h/km)
Depth (m)	Total P levels (µg/L)
Lakeshore development type	
Distance to shore (m)	
Wind exposure (high, low)	

where γ_{00} is the average log odds of success when all level 2 covariates (W_{sj}) are equal to 0 ($s = 1$ to S, where S is the total number of level 2 covariates) and represents a grand-mean value; γ_{sj} is the effect of covariate W_{sj} on the average log odds of success; u_{0j} is the random effect associated with lake j ($u_{0j} \sim N[0, \tau_{00}]$, where τ_{00} is the variance between lakes in lake-average log odds of success. A predicted log odds of success can then be converted to a probability by calculating

$$\varphi_{ij} = \frac{1}{1 + \exp(-\eta_{ij})}. \quad (4)$$

To provide further illustration of the model structure, assume that we are interested in modeling nest success as a function of a single nest-level covariate (level 1), nest depth, and a single lake-level covariate (level 2), LD. The model can be viewed in two levels and in combined form as follows (parameters and subscripts are defined as above):

Level 1:

$$\eta_{ij} = \beta_{0j} + \beta_{1j}(\text{nest depth})_{ij} \quad (5)$$

Level 2:

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\text{LD})_j + u_{0j}, \qquad \beta_{1j} = \gamma_{10} \quad (6)$$

Combined form:

$$\eta_{ij} = \gamma_{00} + \gamma_{10}(\text{nest depth})_{ij} + \gamma_{01}(\text{LD})_j + u_{0j} \quad (7)$$

We performed generalized linear modeling using the GLIMMIX macro of the MIXED procedure in the Statistical Analysis System (SAS; SAS Institute 2000). When many GLMs are used, there is a possibility that the conditional variance of the errors may differ from theory. The GLIMMIX macro allows for the possibility that the conditional error variance differs from theory by adding an additional parameter to the conditional variance, the extra-dispersion parameter (ϕ). If $\phi < 1$, then the distribution of the conditional errors is said to be underdispersed; if $\phi > 1$, then the distribution is overdispersed. If ϕ is close to 1, then the variance is consistent with the assumed distribution (Littell et al. 1996). Underdispersion can lead to inflated standard errors, while overdispersion can lead to underestimated standard errors and thus inflated type I error rates. Therefore, we assessed the final model for over-dispersion or underdispersion by examining the extra-dispersion parameter.

Nest habitat features.—Because we hypothesized that nest depth, substrate type, and the presence or absence of cover would be influenced by anthropogenic effects associated with LD, we modeled these nest attributes as a function of local LD type and

lakewide LD. For nest depth, we used a two-level mixed model that included lake as a random effect and local LD type and lakewide LD as fixed effects. Local LD type was included in the model by designating developed–maintained and developed–retained shorelines as dummy variables (undeveloped shorelines were reference cells). For substrate type and the presence or absence of cover, we used a GLMM with predictor variables designated as above. The analyses were performed with the GLIMMIX macro and MIXED procedure in SAS (SAS Institute 2000).

Nest distribution.—To explore patterns of nest distribution relative to available habitat, we used a chi-square goodness-of-fit test to determine whether the habitat used for nest construction was significantly different from the distributions of available habitat. We reasoned that if most nests were located in a relatively rare habitat type, it would be indicative of high nest site selectivity and potential limitation of preferred nesting habitat. Habitat was categorized into proportions of each development type and wind exposure combination. The analysis was performed for each lake individually.

Results

A total of 178 largemouth bass nests were located during the study period (Table 3). The number of largemouth bass nests located in each lake ranged from 0 (in Blind Lake) to 51 (in North Lake). Because largemouth bass did not spawn in Blind Lake, it was excluded from further analyses. Largemouth bass initiated nest building in early May, and the number of nests peaked in all lakes in mid-May. Both the last new nest and the last successful nest were located on 8 June 2004.

Nest Success

To determine the magnitude of variation among lakes in the probability of nest success, we estimated an

TABLE 3.—The total number of largemouth bass nests and the number of successful and failed nests located at each Michigan study lake. The sum of successful and failed nests is less than the total number of nests because the total includes those nests for which the fate could not be determined. Lakes are ordered according to increasing dwelling density.

Lake	Total number of nests	Successful nests	Failed nests
Blind	0		
Bruin	21	12	5
East Crooked	48	23	9
Halfmoon	24	9	9
North	51	19	18
Patterson	34	10	16

unconditional model with no predictors at the nest or lakewide level. The average log odds of nest success across lakes ($\hat{\gamma}_{00}$) was equal to 0.26. Therefore, the probability of success in an "average" lake (i.e., one with a random effect of $\hat{u}_{0j} = 0$) was 0.56. The variance between lakes in the lakewide average log odds of success ($\hat{\tau}_{00}$) was estimated as 0.193; thus, we would expect that 95% of the lakes in our study have a probability of nest success between 0.35 and 0.75.

Surprisingly, no nest-scale habitat characteristics were significantly associated with the probability of nest success ($P \geq 0.10$). At the whole-lake scale, however, the probability of nest success decreased markedly with increasing LD (intercept [$\hat{\gamma}_{00}$] = 1.96, SE = 0.748, $P = 0.078$; slope, effect of LD [$\hat{\gamma}_{01}$] = -0.096, SE = 0.04, $P = 0.018$). The predicted probability of nest success ranged from 0.77 in Bruin Lake (the lake with the lowest LD) to 0.45 in Patterson Lake (the lake with the highest LD; Figure 2). No other lakewide covariates were significant (all $P > 0.20$). Overdispersion or underdispersion was not evident in our analysis; the extra-dispersion parameter was estimated to be very close to 1 ($\phi = 1.02$; Littell et al. 1996).

Angling Effort

Our estimates of total fishing effort (total angler-hours/km of shoreline) were quite variable among lakes but did not vary predictably with LD in May or June (May: $P = 0.75$; June: $P = 0.21$). Estimated total angler-hours were much lower during the May period (range = 0–227 h/km; SD = 0.0–64.5), when the majority of nesting occurred, than during June (range = 65–453 h/km; SD = 29.3–158.3), when the legal season for black bass fishing was open. Anglers that
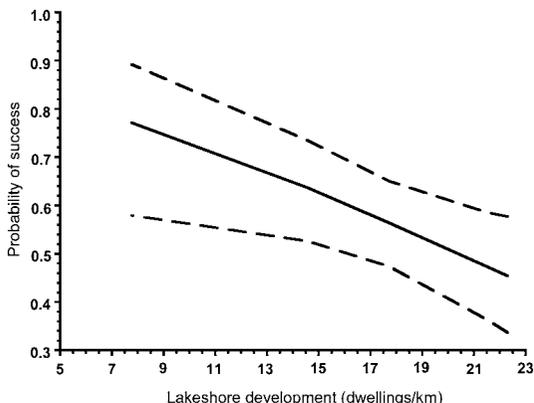

FIGURE 2.—Predicted probability of largemouth bass nest success (solid line) and 95% confidence interval (dashed lines) in relation to residential lakeshore development in five Michigan lakes.

appeared to target black bass represented a substantial component of total angling effort both before and after the opening of the legal black bass season (35% and 42% of angling effort in May and June, respectively). Thus, even though the predominance of angling that potentially targeted nesting black bass increased in June, it still occurred in May to a substantial degree despite the fishing regulations.

Nest Habitat Features

Nest depth was the only nest habitat feature that differed significantly among shoreline development types. Local LD type explained 8.5% of the variation in depth of largemouth bass nests. According to our model, largemouth bass nests constructed near undeveloped shorelines were, on average, found in shallower water than nests constructed near developed shorelines, and nests constructed near retaining walls were, on average, constructed in even deeper water (intercept = 0.845, SE = 0.065, $P = 0.002$; fixed effect of developed–maintained shoreline = 0.135, SE = 0.047, $P = 0.004$; fixed effect of developed–retained shoreline = 0.197, SE = 0.058, $P = 0.0009$). The grand-mean depth at which largemouth bass nests were constructed was 0.92 m (95% confidence interval = 0.83–1.01) and did not vary significantly among lakes (between-lake variance estimate = 0.008, $P = 0.12$). Surprisingly, substrate type and the presence or absence of cover did not significantly differ among either local LD types or among lakes according to lakewide LD.

Nest Distribution

Largemouth bass used shoreline habitats to construct nests in proportions that differed from what was available in four of five lakes (Figure 3), although the patterns of selection varied among lakes. The only lake in which largemouth bass used habitat in proportion to availability was Bruin Lake (7.8 dwellings/km), where the majority of habitat and nest sites were composed of undeveloped shoreline. For East Crooked Lake (14.6 dwellings/km) and Patterson Lake (22.3 dwellings/km), largemouth bass selected undeveloped shorelines for nest construction, as we had expected. In East Crooked Lake, largemouth bass utilized undeveloped sites that were exposed to low and high wind, whereas largemouth bass in Patterson Lake primarily used undeveloped sites in areas of low wind exposure in greater proportion than what was available. Contrary to our expectations, in both Halfmoon Lake (17.7 dwellings/km) and North Lake (21.5 dwellings/km), largemouth bass primarily used developed–maintained shorelines in areas of low wind exposure for nesting. In Halfmoon Lake in particular, largemouth bass nests were located in undeveloped
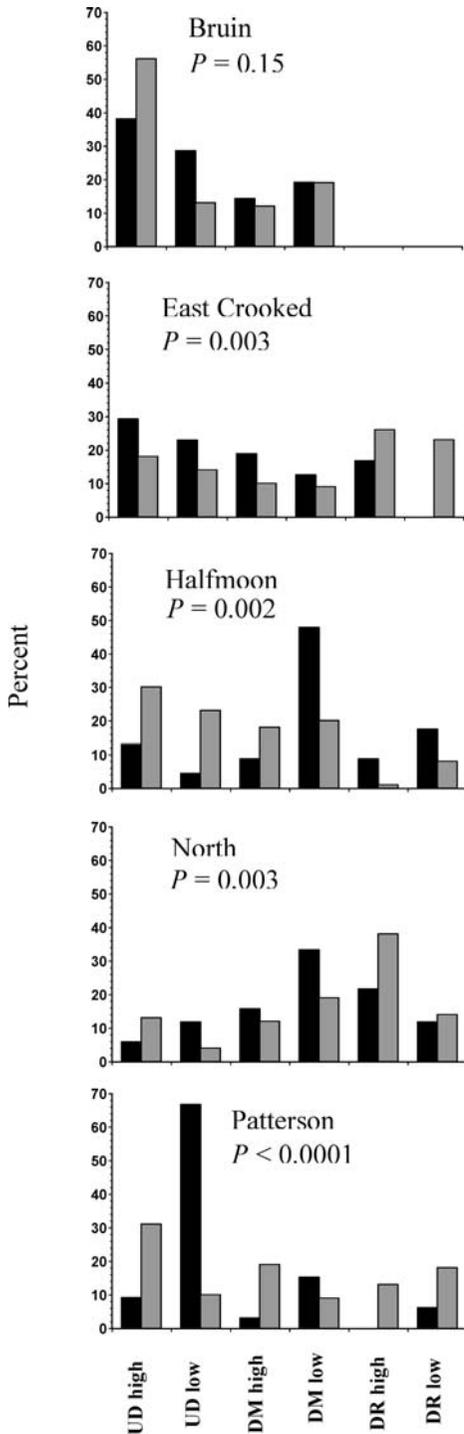
FIGURE 3.—Observed proportions of habitat types used for nest construction by spawning largemouth bass in 2004 (black bars) and proportions of total available habitat types (gray bars) in each of five Michigan study lakes. The P-values are for chi-square goodness-of-fit tests. Lakes are ordered from low to high lakeshore dwelling density. Habitat type codes are as follows: UD = undeveloped shoreline, DM = developed–maintained shoreline, DR = developed–retained shoreline (i.e., with a retaining wall), low = low wind exposure, and high = high wind exposure.

sites less often than expected given the available proportion of this habitat type.

Discussion

We expected local and lakewide features to influence the distribution and success of largemouth bass nests. In particular, we hypothesized that nests would be concentrated along undeveloped shorelines within lakes and that these nests would have a higher probability of success than nests located along developed shorelines. We thought that availability of cover and visibility to anglers (i.e., nest depth) would explain in large part the differences in nest success between developed and undeveloped shorelines. We also expected nest success to vary predictably among lakes and that nest success would decline with increasing lakewide LD due to higher levels of angling pressure and generally lower availability of preferred nesting habitat. As expected, at the whole-lake scale nesting success declined with increasing lakewide LD, but surprisingly whole-lake angling effort could not explain the differences in nest success among lakes. Further, we saw no evidence that local nest features, such as availability of cover or nest depth, could explain variability in success among nests. Patterns of nest distribution relative to available habitat varied among lakes; there was some indication that preferred habitat becomes limiting at high levels of LD but also that additional refinement of habitat categories is required (see Nest Distribution below).

Nest Success

Contrary to our expectations, neither nest depth nor other local nest features could explain a significant amount of variation in nest success. Although this is consistent with findings by Gross and Kapuscinski (1997), who determined that local habitat characteristics such as nest depth and dominant substrate type could not predict smallmouth bass reproductive success in Lake Opeongo, Ontario, Canada, we view these findings as somewhat surprising given the attention in the literature on local nest habitat features and the documented habitat preferences of black bass (Hunt and Annett 2002; Saunders et al. 2002; Wills et al. 2004). Why did we fail to detect local effects on nest success? It may be that a more-detailed quantification of structure is needed. In our field observations, available structure was treated as a categorical variable

(presence/absence) such that we failed to consider varying degrees of cover. For example, an extensive stand of vegetation and a few sprigs of macrophytes in close proximity to nests were considered to be equal vegetative cover, whereas they may in fact influence the fate of an individual nest differently. Also, angling may require observation at a finer (i.e., local) spatial scale (see below). Variation in the abundance and spatial distribution of nest predators (a factor that we did not quantify), both within and across lakes, may play a predominant role in determining variation in nest success. In fact, the interaction between fishing pressure and nest predator abundance may be important, as the removal of guarding male black bass during fishing, even for a brief period of time, increases the probability of nest failure due to predation (Kieffer et al. 1995; Philipp et al. 1997).

Contrary to our expectations, fishing effort did not increase with lake dwelling density. Hence, fishing pressure could not account for the approximate 35% decline in the probability of nest success across lakes. The lack of a positive relation between fishing pressure and dwelling density in our lakes may be related to the fact that all the study lakes have public access. Therefore, many of the anglers probably do not reside on the lakes. Still, we were initially surprised that fishing effort could not explain the variation in nest success, because the effects of fishing on nest success have been investigated in ponds and sections of lakes and there is convincing evidence that fishing negatively affects the success of individual nests (Neves 1975; Ridgway 1988; Kieffer et al. 1995). This reduction in nest success is often due to nest predation that occurs either while the male black bass is off the nest or even after the male black bass has returned, because such males show a decreased ability to defend the nest and an increased likelihood of abandoning the nest (Philipp et al. 1997; Suski et al. 2003).

Our working hypothesis for why fishing effort did not explain a significant amount of variation in nest success relates to the spatial distribution of angling relative to nest distribution. Our angling surveys may have been conducted at too broad of a scale. For example, anglers in Patterson Lake were observed to use methods that targeted nesting black bass in a small cove with a high number of black bass nests. Nest predators also appeared to be particularly abundant in this cove. The nest failure rate in this cove was particularly high. It is likely that the spatial distributions of fishing and of nest predators interact to influence nest success, such that both factors should be observed at finer spatial scales to allow evaluation of their combined effect on nest success. High levels of shoreline development may result in the concentration of nesting black bass and potential nest predators, such as other centrarchid species.

Finally, although we chose lakes that were similar morphometrically, we cannot conclusively rule out the possibility that other unmeasured features of our study lakes (either natural or due to human activities) covaried with LD and provided the mechanism driving the observed negative relationship between nest success and LD. For example, it is possible that some feature of a lake, such as an unmeasured indicator of littoral habitat quality, that makes the lake unfavorable for black bass reproduction also makes it preferable for human development. Future studies examining the relative importance of LD on nest success that include more study lakes and contain more-detailed measurements of habitat will help address such questions.

Nest Habitat Features

We hypothesized that nest habitat features (e.g., nest depth, substrate type, and presence/absence of cover) would vary predictably among local LD types and lakewide LD. Nest depth was the only variable that varied, differing among local LD types. The presence of retaining walls and, to some extent, maintained shorelines apparently reduced the availability of shallow-water spawning habitat, resulting in the construction of largemouth bass nests in deeper water. However, because neither nest depth nor local LD type was significant in predicting nest success, the difference in nest depth among local LD types does not appear to have substantive effects on nesting success. Research has demonstrated that local modification affects substrate type, vegetation cover, and coarse woody material abundance in these lakes and others in Wisconsin and Minnesota (Radomski and Goeman 2001; Jennings et al. 2003; Jubar 2004). Therefore, the fact that these factors did not vary predictably among nest sites according to modification type indicates that largemouth bass effectively seek out these features even if they are relatively less abundant at developed sites.

Nest Distribution

Habitat availability may affect the overall outcome of nesting for a population by altering the number of nests, the distribution of those nests, and the success of those nests in producing swim-up fry. The number of largemouth bass nests that we detected ranged from 0 to 51 across lakes, and five of the six lakes had at least 21 largemouth bass nests. We cannot decisively discern the influence of the abundance of adult male largemouth bass on nest number across lakes; however, largemouth bass catch per effort ranged from 47 to 92 fish/h and was not related to the number of nests located in each lake ($r = 0.28$, $P = 0.59$) or the average

probability of success in each lake ($P = 0.30$; A. K. Jubar and M. T. Bremigan, unpublished data). Determining the potential influence of male largemouth bass abundance on the number of nests and nest success is further complicated by the fact that not all adult males breed during each year (Raffetto et al. 1990).

We reasoned that if nests were disproportionately abundant along undeveloped shorelines and rare along developed shorelines, then local LD influences on nest site choice (or the very early success or failure of nests, i.e., failure before nests were detected) would be indicated. Although local habitat features of nest sites have been studied (Gross and Kapuscinski 1997; Rejwan et al. 1999), to our knowledge the distribution of nest sites relative to local LD status has not been evaluated. Given the propensity of black bass to select nest sites with nearby structure (Bozek et al. 2002; Hunt and Annett 2002), one would expect fewer nests to occur along developed shorelines due to the coarse woody material reduction associated with residential LD, which has been documented in northern Wisconsin lakes (Christensen et al. 1996) and in our study lakes (Jubar 2004).

There was substantial among-lake variation in nest distribution relative to development type. Overall, patterns appeared to roughly correspond to lakewide LD. For example, Bruin Lake, the study lake with the lowest level of development and that also had largemouth bass nests, was the only lake in which nest distribution did not differ from random with respect to development type and wind exposure. From this pattern, we infer that strong selection for development status or wind exposure did not occur. The majority of nests in Bruin Lake were located along undeveloped shoreline, indicating that strong selection was not necessary because the majority of available shoreline was of this type. In contrast, in Patterson Lake, the study lake with the highest level of development, strong selection for nesting along undeveloped shoreline with low wind exposure was evident. The majority (~65%) of nests were located in this category, which comprised only about 10% of the shoreline. In the remaining three lakes, we saw intermediate results, generally involving selection for undeveloped and developed–maintained shoreline and avoidance of developed–retained shoreline. In fact, developed–retained shoreline was avoided in all but one lake (Halfmoon Lake). It may be that additional habitat features must be accounted for to explain the distribution of largemouth bass nests in lakes. For example, in Halfmoon Lake, where nests were concentrated along developed–maintained shorelines with low wind exposure, much of the undeveloped shoreline was of poor habitat quality for nesting and

consisted of shallow (<0.5 m) depths and consolidated, compacted substrates with little cover. Poor "natural" habitat probably also explains the lack of nests in Blind Lake, where most of the littoral substrate consisted of consolidated clay (A. K. Jubar, personal observation). Although the observed patterns did roughly correspond to LD patterns, we cannot rule out other factors that may influence nest distribution. For example, Rejwan et al. (1999) identified a positive relationship between smallmouth bass nest density and temperature and shoreline reticulation in Lake Opeongo.

Conclusions

Elucidation of the spatial scale at which controlling factors operate is a challenge in ecological studies. However, the use of multilevel models as in our study allows for the investigation of potential controlling factors (i.e., covariates) at multiple spatial scales in a single statistical model. We determined that although local habitat characteristics are likely to be important factors affecting nesting success, lakewide features of lakes are also important (actually more important in our study) and help explain large-scale patterns in nesting success that would be missed if only local habitat characteristics or single lakes were considered.

Understanding the ecology and management of black bass is challenged by the disconnect between the effects of fishing and habitat on individual nests and the ultimate population-level effects. Certainly, events after nesting are also important contributors to recruitment. To date, most research on black bass nesting success has been done in ponds or sections of lakes in an experimental context. Such work is important, but it does not quantify the magnitude of anthropogenic and natural effects at the whole-lake scale. Our findings demonstrate that dwelling density warrants more attention. Our study provides valuable information for modelers by quantifying the scope of the response, and hence it begins to define the compensatory capacity (in subsequent life stages) needed to nullify negative effects of lakeshore dwelling density on nest success. This constitutes a critical step in ultimately determining the population-level effects of habitat modification and fishing on black bass recruitment.

Acknowledgments

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