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Habitat Features Affecting Smallmouth Bass *Micropterus dolomieu* Nesting Success in Four Northern Wisconsin Lake

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Abstract.—Evaluating spawning success in relation to habitat characteristics of nests sites provides critical information necessary to assess the effects riparian and littoral zone habitat alterations have on smallmouth bass *Micropterus dolomieu* survival and recruitment. The objective of this study was to quantitatively evaluate smallmouth bass nest site quality in lakes in order to evaluate the importance habitat features have on nesting success. We evaluated smallmouth bass egg survival and fry production as a function of nest characteristics in four northern Wisconsin lakes from 1998 to 2000 using simple and multiple linear regression analyses. Mean smallmouth bass egg survival and fry production were significantly different (analysis of variance [ANOVA]) among lakes; nests in Big Crooked and Bear Lakes had higher egg survival and fry production than Pallette and Sanford Lakes. Relations were variable among lakes, indicating that no single habitat feature consistently predicted nest success across lakes. Habitat features accounted for up to 27 percent (distance to nest cover) of the variation in egg survival and 50 percent (diameter of nearest log cover) of the variation in fry production. Measures of substrate size were the most predominant nest characteristic associated with variation in both egg survival and fry production among lakes but they were not significant in all lakes. Other features related to nest cover, nest position, and morphology explained some variation in egg survival and fry production but they were inconsistent across lakes. This study shows that habitat characteristics affecting smallmouth bass nesting success are extremely variable across lakes and will require further study to elucidate how habitat quality influences nesting success.

Introduction

Spawning habitat is important to reproductive success and recruitment of smallmouth bass *Micropterus dolomieu* (Neves 1975; Serns 1984; Lukas and Orth 1995, Sowa and Rabeni 1995). However, few studies have explicitly examined reproductive success in relation to habitat features at the individual nest scale in lakes even though linking environmental conditions to demographic features of populations (i.e., reproduction) is critical to understanding population dynamics (Garshelis 2000). Such studies of habitat quality are uncommon in aquatic systems (Hall et al. 1997; Garshelis 2000).

Previous studies provide general descriptions of nesting habitat use. Smallmouth bass generally use gravel substrates but may use sand, silt, and organic material and are usually associated with rock or woody cover (Scott and Crossman 1973, Winemiller and Taylor 1982, Reynolds and O'Bara 1991). Rejwan et al. (1999) showed that factors such as shoreline complexity and temperature helped explain the distribution of nests at the whole-lake scale. However, while general habitat use has been investigated, the relations between nest-scale habitat features and nesting success are unclear and largely untested in lakes. Moreover, other factors (e.g., behavior, climate) can also influence nesting success that may confound discrete relations between nest characteristics and nesting success. For instance, Lukas and Orth (1995) found that temperature and streamflow masked the effects of habitat conditions influencing smallmouth bass recruitment in a Virginia stream while Wiegmann and Baylis (1995) found that size and behavior of parental males also influence nesting success. At the population level, effects of temperature, water flow, and water level have been modeled with computer-based simulations (Shuter et al. 1980; Jager et al. 1993) but these studies had no experimental validation.

Smallmouth bass occur in a wide variety of lakes and streams having variable physical characteristics throughout their native range. Distinct locations of nest aggregations (Rejwan et al. 1997) and inter-year, site fidelity in spawning adults (Ridgway et al. 1991) suggest that smallmouth bass may select for specific spawning habitat features in these areas such as substrate size, embeddedness, and proximity to cover which may mediate fry production at the nest scale. Moreover, populations likely have adapted toward selecting the best habitat and thus habitat quality may mediate survival of eggs and fry (Morrison et al. 1992). However, surprisingly little is known about microhabitat features of smallmouth bass nests and the quantitative relations between these habitat features and egg survival or fry production at the nest scale in lakes. This information may be lacking because gathering the necessary measures of both relative nest success and habitat features requires specialized equipment (i.e., SCUBA gear), is extremely labor intensive, and costly. However, this information is necessary to understand how changes in habitat may affect smallmouth bass population dynamics. Therefore, the objectives of this study were to assess nest scale habitat features affecting juvenile smallmouth bass survival and fry production in four lakes with varying habitat features.

Methods

Study Area

Big Crooked, Sanford, Bear, and Pallette lakes are glacial lakes located in north-central Wisconsin. All four lakes have limited access and very little development along their shorelines, although the lakes differ in surface area and predominant substrates in littoral zones (Table 1; Figure 1). Big Crooked, Sanford, and Bear Lakes are privately owned. Angling in these lakes is limited to members only and release of all smallmouth bass is required. Pallette Lake is located in the Northern Highland Fishery Research Area and access is limited to walk-in only. Here, smallmouth bass fishing is by permit only and harvest is limited to fish in excess of 40.6 cm (16 inches). Smallmouth bass harvest from Pallette Lake is documented through a comprehensive year-round creel census and therefore, smallmouth bass harvest was accounted for in analyses of nest success.

Data Collection

Smallmouth bass nest site location, habitat characteristics, and nesting success were documented on all lakes during the smallmouth bass spawning seasons from 1998 to 2000. Each lake was surveyed and all nests visited every other day until all smallmouth bass had nested and fry emerged from all

Table 1. Morphological and limnological features of the four study lakes. Woody cover represents the number of pieces of large woody structure (a minimum 1 m long × 15 cm diameter) found per quadrat (m^3). Values in parentheses indicate the actual number of pieces and the actual number of quadrats surveyed. Color was determined using Platinum Cobalt units.

Lake feature	Big Crooked Lake	Sanford Lake	Bear Lake	Pallette Lake
Surface area (ha)	276	36	31	70
Maximum depth (m)	12	16	10	18
Woody cover [number of pieces/number of quadrats (m^2)]	0.05 (174/3380)	0.38 (428/1139)	0.11 (136/1171)	0.04 (141/3460)
Shoreline slope (%)	0.046	0.143	0.130	0.049
Color (Pt units)	8.9	30.4	27.8	14.5
pH	7.1	5.9	7.9	6.6
Total alkalinity (mg/L)	14.0	6.0	91.1	9.0

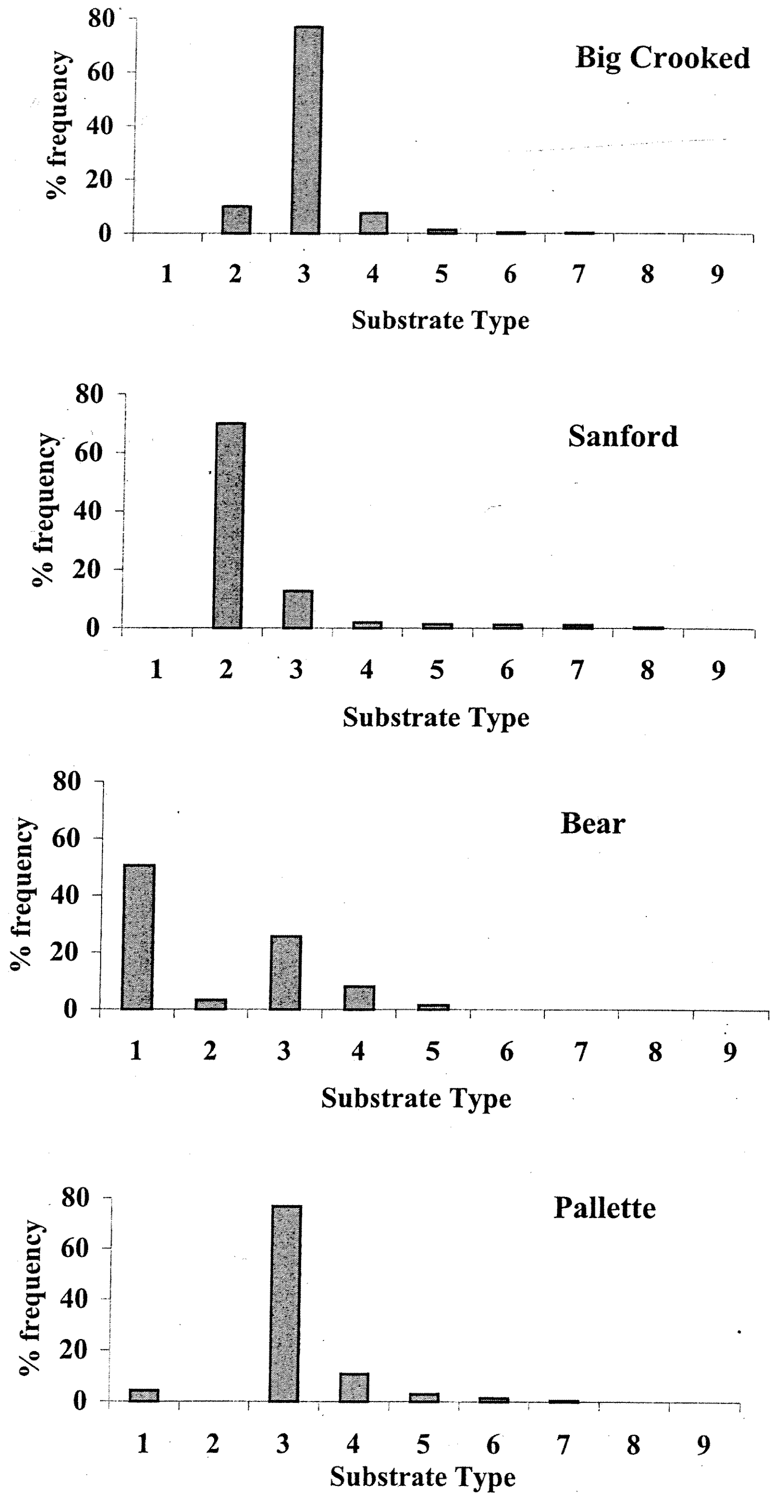

Figure 1. Substrate particle size distributions from the littoral zones of four lakes. (1) fine organic material, (2) silt, (3) sand, (4) gravel, (5) cobble, (6) rubble, (7) small boulders, (8) large boulders, and (9) bedrock.

nests. Smallmouth bass nests were located using several methods. First, nests were located by slowly boating around the entire margin of each lake and visually observing the shallow water (<2 m) for nests using polarized sunglasses. Nests were also located by snorkeling and by towing scuba divers around the 2 m and 3 m depth contour of each lake. Scuba gear was necessary to locate deeper nests (2–3 m). Previous work at the study lakes had demonstrated that 3 m was the maximum depth to which smallmouth bass nests are located and additional surveys beyond this depth contour were conducted to reconfirm this distributional pattern. After locating each nest, a uniquely numbered flag was placed on the lake bottom near the nest. Each nest was also marked on a map of the lake to facilitate relocation for subsequent data collection.

Habitat and biological data at each nest were collected using scuba gear. Egg estimates were visually conducted using a 30 cm × 30 cm grid composed of 25 smaller (6 cm × 6 cm) squares. This grid was placed across the top of the aggregation of eggs. The number of eggs in each smaller square was estimated then later summed for an overall nest estimate. Fry estimates were conducted in a similar manner but using a larger (36 cm × 36 cm) grid with 36 (6 cm × 6 cm) squares. The larger grid was necessary as fry covered a larger area in the nest. Fry estimates were standardized by stage of development (Hubbs and Bailey 1938); fry estimates were conducted only after they had black pigmentation prior to swim-up. At this time, fry briefly orient themselves on top of the substrate in the nest before they begin to disperse to forage.

Egg and fry estimates were validated by comparing the number of eggs or fry estimated using the grid to an actual count conducted on a subsample of 12 nests (6 for egg estimates, 6 for fry estimates). For validating estimates, we carefully removed all eggs or fry from each nest using suction, removed all substrates to ensure inclusion of all eggs or fry, and counted all eggs or fry after each estimate. Linear regression was then used to determine the accuracy of the estimate (i.e., coefficient of determination). A slope of 1.0 indicates that on average, the estimate reflects the true number of eggs or fry. For analyses, estimates were corrected by multiplying the egg or fry estimate by the inverse of the regression slope that relates the actual number of eggs or fry on the nest to the estimated number of eggs or fry on the nest. The intercepts were not significantly different than zero and thus were not used in the correction. Eggs and fry were immediately placed back into the nest after the validation, though these nests were not used in subsequent analyses of nest success.

Immediately after fry emergence, habitat characteristics from each nest were quantified and used to predict survival and fry production. Habitat features used as predictor variables included nest diameter, nest depth, distance from shore, slope, distance to nearest active nest, substrate size, substrate embeddedness, cover type (i.e., rocks and woody structure), size of nearest cover, proximity to cover, and position of nest relative to cover (e.g., under, adjacent, none). Percentages of each substrate size (Wentworth 1922; Platts et al. 1983) were visually estimated. Embeddedness of each substrate category was also visually qualified as the degree to which fine substrate was embedded in the nest matrix. We used a system modified from Platts et al. (1983) whereby highly embedded substrates were coded as 4 and clean substrates were coded as 0 (Saunders 2002). Nest cover was also quantified at each nest. Cover was included in analyses if it was located less than 1.5 m from the rim of the nest. Distance to, and dimensions of, large rocks and logs used for cover were measured. Nest orientation to cover was evaluated as proximal (within 1.5 m but not adjacent or under), adjacent (rim of nest touches cover or intersect a vertical plane of the nest rim edge), or under (egg portion of nest lies beneath cover). Shoreline slope was measured at two scales. General shoreline slope at the nest site was measured by dividing the depth from the deep rim of the nest by the distance to the shoreline water interface. Nest site slope was more specific and measured as the difference between water depth 2 m from the nest towards shore and 2 m from the nest away from shore divided by the linear horizontal distance between those depth measurements.

Analyses

Regression analyses were performed using two dependent variables, each representing a different measure of nest success: egg survival and fry production. Egg survival represented the percentage of eggs that survived to swim-up fry off each nest and was calculated as

$$\text{Egg survival} = (\text{\# of fry}/\text{\# of eggs}) \times 100$$

In contrast, fry production represented the total number of fry in each nest immediately prior to swim-up at the black fry stage of development. Actual values used were the number of black fry corrected for estimate bias using the validated regression equation. Production represented the overall count of fry and was not indexed relative to eggs as was done for egg survival.

We used simple and multiple linear regression to assess the importance of each habitat feature in explaining variation in nest success in each lake. Models were significant at *P* less than or equal to 0.05. Independent variables and fry production were transformed using log, inverse, and square root transformations to normalize residuals, when appropriate (Neter et al. 1996). Survival was transformed using an arcsine transformation, when necessary. We assessed fit using the coefficient of determination and diagnostically examined residuals of regression analyses to select the best transformation for each model. We used ANOVA of ranked values and Scheffé multiple range tests to assess differences in egg survival, fry production, lengths of parental males, and nest characteristics across lakes. Alpha was set at *P* less than or equal to 0.05.

Results

Egg and fry visual estimates were quite accurate in enumerating actual numbers of eggs and fry on nests (Figure 2). Coefficients of determination were 0.98 for egg estimates and 0.97 for fry estimates. Slopes of both lines were less than 1.0 indicating that estimates slightly underestimated the actual number of individuals on the nest. Examination of residuals showed no systematic bias in the estimates occurred relative to the number of eggs or fry in nests.

Demographic features of smallmouth bass in each lake were variable across lakes but were similar among years for Big Crooked Lake (Table 2). Adult smallmouth bass population densities were lowest in Big Crooked Lake (0.6–0.8 adults per hectare) and highest in Pallette Lake (10.3 adults per hectare). Parental male size structure also varied across lakes with the largest males found in Big Crooked Lake (ANOVA $F = 12.956$, $P < 0.001$) (Figure 3).

Littoral zone habitat differed substantially in each lake (Figure 1). In Big Crooked and Pallette Lakes, littoral zone substrates were dominated by sand, but had coarser gravel and cobble substrates. In Sanford and Bear Lakes, finer substrates such as silt and organic matter were common in the littoral zone but coarser substrates were almost completely absent. Cover in littoral zones also differed among lakes. Big Crooked and Pallette Lakes had few boulders or pieces of coarse woody structure whereas the littoral zones of Sanford and Bear Lakes had abundant coarse woody structure and few boulders. Unlike other lakes, Bear Lake also had substantial macrophyte beds along much of the shoreline.

Habitat characteristics associated with smallmouth bass nests varied across lakes (Table 3). Nests in Big Crooked Lake were composed almost entirely of gravel and cobble whereas nests in the other study lakes were composed mostly of gravel and sand. In fact, 19 percent of nests in Pallette Lake had greater than or equal to 50 percent sand with four nests being composed entirely of sand. The mean percentage of sand in the nest was similar (24–31%) in Sanford, Bear and Pallette Lakes. In contrast, percentages of sand in Big Crooked Lake nests rarely exceeded 20 percent even though sand is the dominant substrate in the littoral zone. Substrates outside of the actual nests reflected the general spawning area characteristics. Coarse substrates were located outside nests in Big Crooked Lake whereas finer substrates occurred outside nests in the other lakes. Similarly, embeddedness of nests reflected substrate composition of the general spawning area. Big Crooked Lake had the least embedded nests whereas Pallette, Sanford, and Bear Lakes had higher mean embeddedness values.

Table 2. Demographic features of smallmouth bass populations in the study lakes. Population estimates include 95% confidence intervals in parentheses.

Lake	Big Crooked 1998	Big Crooked 1999	Big Crooked 2000	Sanford 1998	Bear 1999	Pallette 2000
Adult population estimate	168 (93–336)	233 (114–837)	207 (82–518)	165 (108–264)	79 (43–198)	722 (492–1243)
Adults per hectare	0.6	0.8	0.8	4.6	2.5	10.3
Number of nests	38	49	48	51	28	107
Nests per shoreline km	3.5	4.5	4.4	9.6	6.1	26.6
Mean (± S.E.) distance	44.3 ± 5.3	46.2 ± 9.1	40.0 ± 5.0	46.0 ± 5.6	23.9 ± 7.0	18.6 ± 1.5

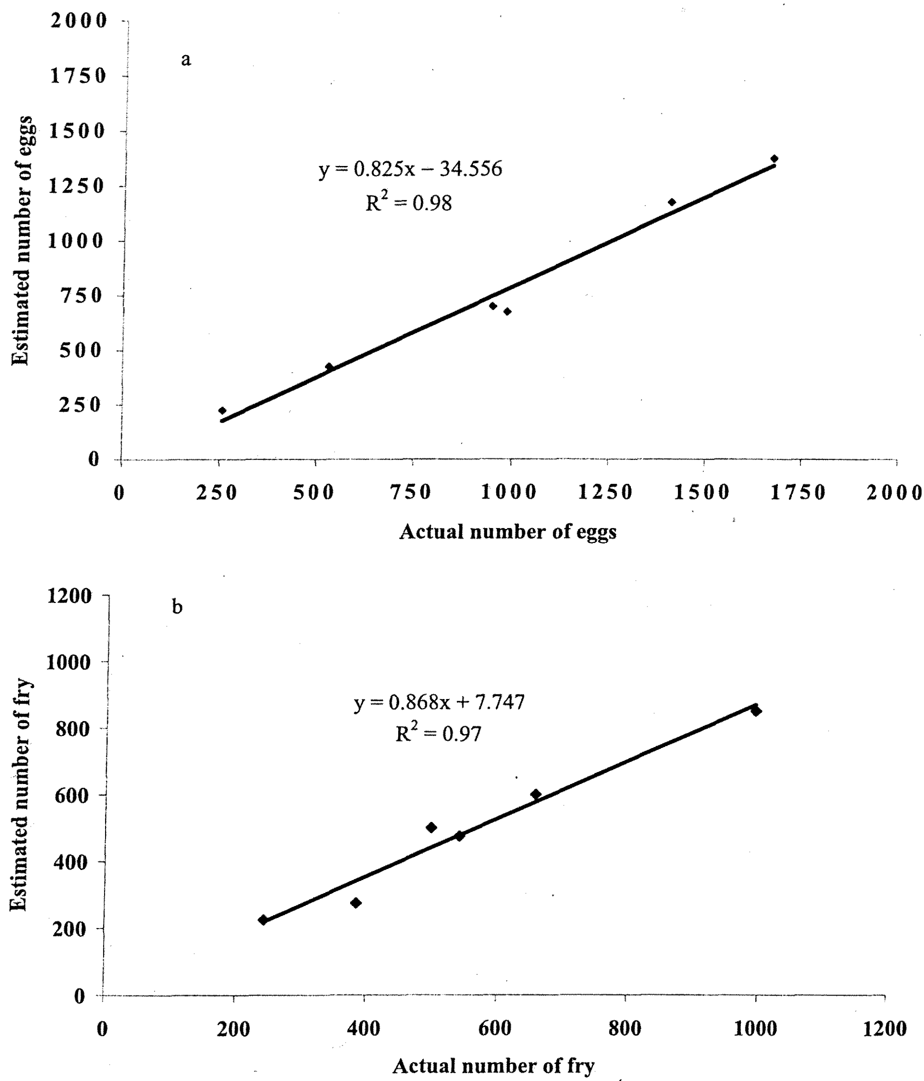

Figure 2. Relations between estimated number of eggs (panel a) and fry (panel b) on the nest using a 30 cm × 30 cm and 36 cm × 36 cm grid, respectively, and the actual number counted after full removal from nest. Note different scale on graphs.

Although limited in supply, large rocks and small boulders were consistently used as cover (74% of nests) for nesting males in Big Crooked Lake. In contrast, only two to four nests were placed near woody structure in Big Crooked Lake each year. The opposite was true in Sanford and Bear Lakes where 78 and 100 percent of nests respectively, were placed next to woody structure. In Pallette Lake, 36 percent of nests are placed near woody structure, 32 percent of nests are placed near a rock, 21 percent of nests are placed near woody structure and a rock, and 11 percent of nests were not close to any cover at all.

Nesting Success

Both survival and fry production were variable across lakes, and in Big Crooked Lake, also across years (Figure 4). Overall, nests in Big Crooked and Bear Lakes had the highest ranked mean egg survival; Sanford Lake had the lowest. Survival did not vary across years in Big Crooked Lake (ANOVA $F = 1.028$, $P = 0.361$).

Habitat features affecting egg survival were variable across lakes and, in Big Crooked Lake, also across years (Table 4). No variable was a significant predictor of egg survival across lakes. In

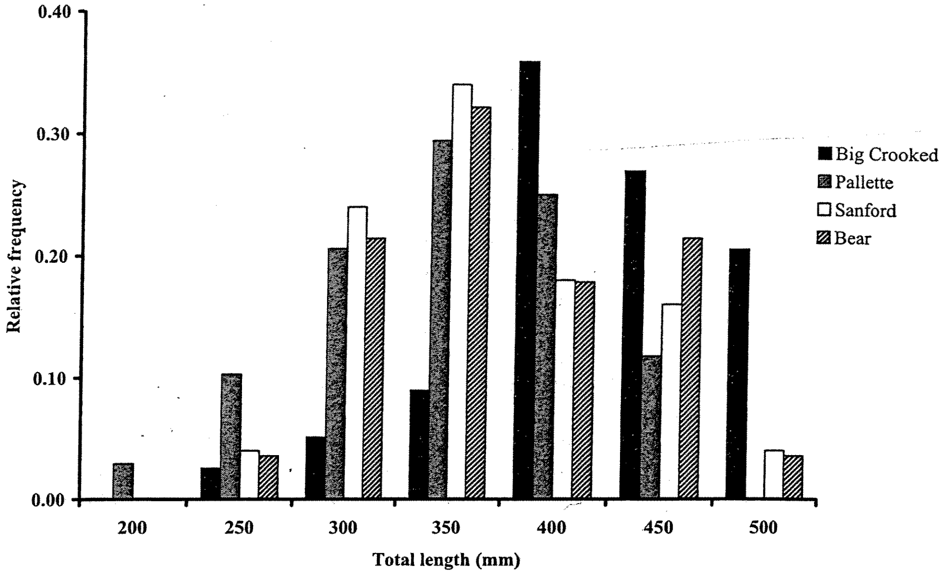

Figure 3. Distribution of total lengths (mm) of parental male smallmouth bass on active nests in four north temperate lakes. Lengths were similar across years (1998–2000) in Big Crooked Lake and were pooled (ANOVA $F = 1.028$, $P = 0.361$).

fact, few variables were significant in more than one lake. Our best models predicting survival were univariate relations accounting for between 0 and 27 percent of the variation in egg survival based on habitat features (Tables 4 and 5). Nest substrate size was the most consistent predictor of egg survival in Big Crooked and Sanford Lakes but not in Pallette and Bear Lakes. In Big Crooked (1999), Big Crooked (2000), and Sanford lakes, percent cobble in the nest was significantly related to egg survival. Difference to cover was significantly related to egg survival in Pallette Lake, whereas cover was not significant in Big Crooked, Sanford Lake, and Bear Lake. In Pallette Lake, the distance to cover was negatively related to egg survival accounting for 27 percent of the variation in survival. IThe only other prominent habitat feature affecting egg survival was the distance to the nearest active nest in Big Crooked Lake in 1998. No multiple regression models were significantly related to egg survival in any lake.

As with egg survival, fry production also var-

Table 3. Differences in physical characteristics of smallmouth bass nests in the littoral zone of four north temperate lakes. Values represent the mean ± 1 standard error. Characteristics of nests in Big Crooked Lake were not significantly different across years and, thus, values were pooled. Statistically different groups are noted with lowercase letters (Ranked ANOVA, Scheffe's multiple-range test, Apha was set at $P \leq 0.05$).

Nest characteristic	Big Crooked Lake	Sanford Lake	Bear Lake	Pallette Lake	F	P
Nest diameter (m)	0.93 ± 0.03	0.68 ± 0.02	0.56 ± 0.03	0.52 ± 0.03	54.5	< 0.001
Sand (%)	5 ± 0.9	31 ± 3.9	24 ± 3.5	26 ± 2.8	27.7	< 0.001
Gravel (%)	75 ± 1.9	63 ± 4.1	70 ± 4.1	62 ± 2.8	6.1	< 0.001
Cobble (%)	19 ± 1.8	5 ± 1.0	6 ± 1.3	6 ± 1.1	15.1	< 0.001
Substrate embeddedness	1.2 ± 0.1	2.6 ± 0.1	3.0 ± 0.1	2.4 ± 0.1	46.5	< 0.001
Percent nests near rocky cover	74	10	0	32		
Percent nests near woody cover	11	78	100	36		
Percent nests near both rocky and woody cover	14	6	0	21		
Percent nests with no cover	0	6	0	11		

ied across lakes, but in Big Crooked Lake, it also varied across years. Nests in Big Crooked Lake in 1998 had higher mean levels of fry production than in other lakes or other years in Big Crooked Lake. Big Crooked (1999 and 2000) and Bear lakes had intermediate levels of fry production. Nests in Sanford and Pallette Lakes had the lowest mean fry production.

Habitat features affecting fry production were variable across lakes and, in Big Crooked Lake, also across years (Table 6). In general, substrate was a better predictor of fry production in Sanford and Pallette Lakes than in Big Crooked or Bear Lakes. All four metrics of nest substrate were significantly related to fry production in Sanford and Pallette Lakes whereas only one metric of nest substrate was significantly related to fry production in Big Crooked Lake in 1998 and 1999 as well as in Bear Lake. No metrics of substrate were significantly related to fry production in Big Crooked Lake in 2000.

Cover was significantly related to fry production only in Pallette Lake and Bear Lake. In Pallette Lake, only the percentage of the nest that was under a log was significantly related to nest fry production. In Bear Lake, the diameter of the nearest log accounted for 50 percent of the variation in fry production. This was the strongest relation between any habitat feature and fry production that we found across all lakes and all variables.

Other prominent habitat features affecting fry production were also variable. Distance to shore, nest concavity, and slope were all significantly related to fry production in Big Crooked Lake in 1999, but these relations were not consistent across years. The only other significant relations among lakes were nest diameter in Pallette Lake and distance to shore and nest depth in Bear Lake.

Unlike models for egg survival, our best models predicting fry production were either univariate or bivariate models (Table 7). We could account for between 0 and 50 percent of the variation in fry production based on habitat with our best models. No single habitat feature was significant more than once across lakes in our best models. We could account for more of the variation in fry production in Sanford and Bear Lakes than in Big Crooked and Pallette Lakes. In Sanford and Bear Lakes, models accounted for between 43 and 50 percent of the variation in fry production, whereas in Big Crooked and Pallette Lakes, models only accounted for between 0 and 25 percent of the variation in fry production.

Discussion

Previous studies have identified ecological processes and general lake features influencing survival and recruitment of smallmouth bass. Several researchers have examined the relation between parental male size and nesting success. Neves (1975) and Ridgway and Friesen (1992) found that larger males produce larger broods. This is not surprising since larger males procure more eggs (Wiegmann et al. 1992). Behavioral attributes of

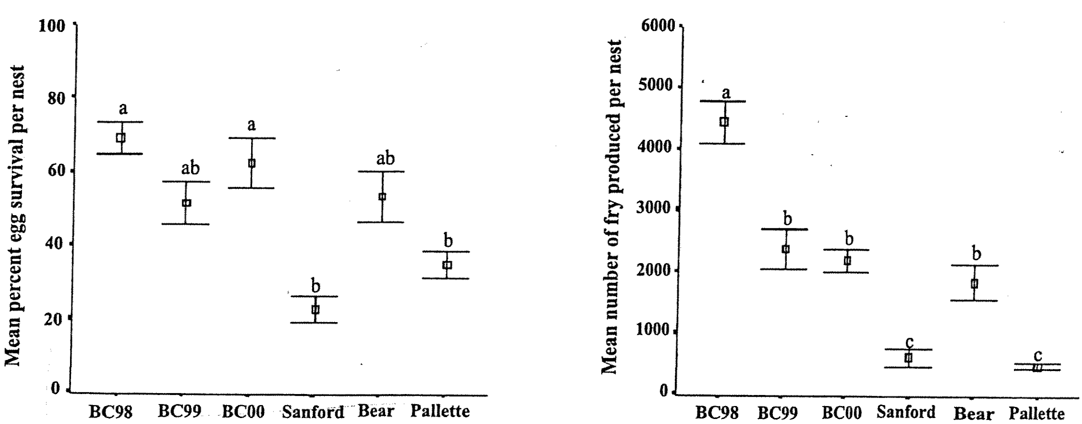

Figure 4. Differences in mean smallmouth bass survival from egg through black swim up fry (per nest) and fry production (per nest) (±1 SE) among study lakes. Mean ranked survival and fry production (ranked ANOVA and Scheffe's multiple range tests) were significantly different ($F = 13.4$, $P < 0.001$, $F = 43.2$, $P < 0.001$, respectively) among lakes. Lakes are: (BC98) Big Crooked Lake 1998, (BC99) Big Crooked Lake 1999, (BC00) Big Crooked 2000.

Table 4. Habitat features found to be significantly related to egg survival at the nest scale. Values reported are coefficients of determination for significant relations. Alpha was set at P < 0.05.

	Lake					
	BC 98	BC 99	BC 00	Sanford	Bear	Pallette
Substrate						
Percent sand in the nest	–	–	–	0.19	–	0.08
Percent gravel in the nest	–	–	–	–	–	–
Percent cobble in the nest	–	0.14	0.24	0.25	–	–
Average embeddedness	–	–	–	–	–	–
Cover						
Nearest cover size	–	–	–	–	–	–
Distance to cover	–	–	–	–	–	0.27
Percent of nest located under a log	–	–	–	–	–	–
Other prominent features						
Distance to shore	–	–	–	–	–	–
Nest concavity	–	–	–	–	–	–
Slope	–	–	–	–	–	–
Nest diameter	–	–	–		–	–
Nest depth	–	–	–	–	–	–
Distance to nearest nest	0.16	–	–	–	–	–

parental males have also been well documented. Ridgway (1988) found that the tenacity of parental male guarding behaviors increased with brood development while Wiegmann and Baylis (1995) found the opposite to be true. In addition to these demographic and behavioral characteristics, habitat features are also thought to affect smallmouth bass nesting success. Early descriptive studies (Hubbs and Bailey 1938; Pflieger 1966) noted that spawning habitat of smallmouth bass was likely mediating recruitment although quantitative analyses were lacking. These studies identified habitat features such as nesting substrate and cover as important in sustaining a healthy smallmouth bass fishery. Lukas and Orth (1995) quantitatively examined differences between successful and unsuccessful nests in a Virginia stream and found that physical habitat features did not differ between successful and unsuccessful nests. However, these findings are not transferable to lentic systems because stream flow was the primary cause of nest failure. Rejwan et al. (1999) found that habitat features significantly affect nest site distribution in lakes but did not examine relations between habitat and nesting success.

The objectives of our study were to quantitatively evaluate the relations between nest site habitat features and nest success measured both in terms of survival and fry production. We found all dimensions of smallmouth bass nesting habitat (i.e., nesting habitat use and nesting habitat quality) to be extremely variable. Habitat features in each of the study lakes were quite different. Littoral zone substrates in Big Crooked Lake are dominated by sand yet sand was rarely found to be a major nest component in this lake. Sand is also quite common in the littoral zones of Pallette, Sanford, and Bear Lakes and in these lakes sand was quite abundant

Table 5. The best regression models for each lake using habitat features to predict smallmouth bass egg survival. All variables in models are significant at $P \leq 0.05$.

Lake	Year	Model	R^2	Model P
Big Crooked	1998	arsin(survival) = 1.17 – 5.67 × log (distance to nearest nest)	0.16	0.028
Big Crooked	1999	survival = 0.41 + 0.05 × sqrt (percent cobble)	0.14	0.049
Big Crooked	2000	arsin(survival) = 1.42 – 0.60 × log (percent cobble)	0.24	0.048
Sanford	1998	arsin(survival) = 0.14 + 0.02 × (percent cobble)	0.25	<0.001
Bear	1999	–		
Pallette	2000	arsin(survival) = 0.27 + 0.43 × (nearest distance to cover)	0.27	0.003

Table 6. Habitat features found to be significantly related to fry production at the nest scale. Values reported are coefficients of determination for significant relations. Alpha was set at $P < 0.05$.

	Lake					
	BC 98	BC 99	BC 00	Sanford	Bear	Pallette
Substrate						
Percent sand in the nest	–	–	–	0.20	0.26	0.20
Percent gravel in the nest	–	–	–	0.13	–	0.08
Percent cobble in the nest	–	–	–	0.35	–	0.06
Average embeddedness	–	–	–	0.23	–	0.12
Cover						
Nearest cover size	–	–	–	–	0.50	–
Distance to cover	–	–	–	–	–	–
Percent of nest located under a log	–	–	–	–	–	0.14
Other prominent features						
Distance to shore	–	0.19	–	–	0.24	–
Nest concavity	–	0.17	–	–	–	–
Slope	–	–	–	–	–	–
Nest diameter	–	–	–	–	–	0.13
Nest depth	–	–	–	–	0.39	–
Distance to nearest nest	–	–	–	–	–	–

in smallmouth bass nests.

Nesting cover was also quite different across lakes but unlike substrate, cover use did seem to reflect relative availability in each lake. Most nests in Big Crooked Lake were near small boulders, nests in Pallette Lake were near small boulders and woody structure, and nests in Sanford and Bear Lakes were near woody structure almost exclusively.

Survival and fry production were variable across lakes and across years in Big Crooked Lake. The range of survival in all study lakes was 0–100 percent (nest failures quantified in this study were the result of fungus infestation with a guarding male still present and not abandonment). At present, no other published literature exhibits this degree of variability in egg survival in smallmouth bass nests. Most likely, this is because very few studies have examined egg survival at the nest scale and those that have examined egg survival have extremely small sample sizes. The ranges of fry production in Big Crooked Lake (0–9,570) and Sanford Lake (0–6,330) were similar to those reported by Neves (1975) (451–7,856) and Ridgway and Friesen (1992) (400–7,000), while the ranges of fry production in Pallette Lake (0–1,900) and Bear Lake (0–4,296) were similar to other studies by Surber (1942) (1,525–3,148), Pflieger (1966) (1,651–3,952), Clady (1975) (175–2,608), and Lukas and Orth (1995) (98–1,802).

Habitat features related to survival and fry production were variable across lakes and across years in Big Crooked Lake. Significant associations between habitat features and survival accounted for between 8 and 27 percent of the variation in survival. No single habitat feature consistently predicted survival across lakes. Significant associations between habitat features and fry production accounted for between 6 and 50 percent of the variation in fry production. In Big Crooked Lake (2000), there were no habitat features significantly associated with fry production. In two lakes, multiple regression models accounted for a greater portion

Table 7. The best regression models for each lake using habitat features to predict smallmouth bass fry production. All variables in models are significant at $P \leq 0.05$.

Lake	Year	Model	R^2	Model P
Big Crooked	1998	—		
Big Crooked	1999	fry = 1238.943 + 20.094 × (distance to shore)	0.19	0.017
Big Crooked	2000	—		
Sanford	1998	log(fry) = 1.81 + 0.04 × (percent cobble) + 1.03 × (nest diameter)	0.44	<0.001
Bear	1999	log(fry) = 2.64 + 1.91 × (nearest log diameter)	0.50	0.001
Pallette	2000	log (fry) = 2.79 – 0.01 × (percent sand)	0.18	<0.001

of the variation in fry production than the best univariate model in those lakes.

Fry production was more predictable in Sanford and Bear Lakes than in Big Crooked and Pallette Lakes. Multiple regression models accounted for between 43 and 50 percent of the variation in fry production based on habitat alone in Sanford and Bear Lakes. However, habitat features only accounted for between 0 and 25 percent of the variation in fry production in the Big Crooked and Pallette Lakes. In Big Crooked Lake, low population density may result in parental males selecting only "high" quality nest sites. This may result in low variation in independent variables that we used to model nesting success. Consequently, few of the models are significant and those that are significant predict little of the variation in fry production. Higher population densities, negative relations between sand and fry production, and the sheer abundance of sand and finer substrates in Pallette, Sanford, and Bear Lakes all suggest competition for high quality nest sites.

Habitat features associated with survival were different than those features associated with fry production. Only 5 of 11 habitat features were consistent predictors of either survival or fry production. This result could be from a variety of factors. First, there is the effect of parental male size and behavior. Larger males often have larger broods (Neves 1975), larger males have the ability to procure more eggs from females (Wiegmann et al. 1992), and larger males may also defend their broods more aggressively than smaller males (Philipp et al. 1997). Random chance alone suggests that more eggs will translate to more fry so it should not be surprising that the factors affecting survival are not necessarily identical to those factors affecting fry production.

This study provided insight into habitat features affecting smallmouth bass survival and fry production. Yet there is still a great deal of work to be done. There is increasing concern over how anthropogenic factors may affect smallmouth bass recruitment (Ridgway and Shuter 1997). Direct and indirect alterations to habitat (i.e., shoreline development and riparian/upland land-use practices) (Jennings et al. 1999), eutrophication (Haines 1973), decreasing amounts of woody structure (Christensen et al. 1996), and increased angling pressure (Kieffer et al. 1995; Philipp et al. 1997) threaten current and future smallmouth bass populations. Understanding how habitat affects survival in the nest is prerequisite to not only developing predictive models, but also to developing strategies to protect prime spawning areas and techniques to restore degraded smallmouth bass spawning habitat. Our results show that different processes appear to be regulating survival and fry production at the nest scaleindicating that different processes may regulate smallmouth bass recruitment in each of these lakes as well. We believe that a good understanding of limnological, habitat, and biological features of each and every lake is essential before we can begin to thoroughly understand how habitat quality affects smallmouth bass recruitment dynamics and how changes to littoral zones may affect smallmouth bass populations.

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