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Enhancing Largemouth Bass Spawning: Behavioral and Habitat Considerations

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Abstract.—Fisheries managers may manipulate littoral habitat to enhance spawning of *Micropterus* basses, but the success of these efforts is affected by habitat preferences and behavior of spawning adults. Largemouth bass *Micropterus salmoides* nest-site selection ($N >$ 600 nests), parental behavior, habitat availability, and the distribution and behavior of potential brood predators were studied in small lentic systems. These data were used to assess the effectiveness of habitat manipulation in these systems (ponds, a kettlebasin lake, and a small impoundment). Parental males demonstrated distinct habitat preferences that were consistent among systems, but were influenced by local conditions. Parental behavior was affected by the abundance of intruders into nest territories, which was influenced by the complexity of physical structure associated with nest sites. Potential brood predators were most abundant in habitat containing complex physical structure. Success of habitat enhancement was affected by factors occurring at two scales: correspondence of the added physical structure with the types of structure normally encountered in the system (microhabitat); and its placement within the littoral zone (mesohabitat). We recommend that managers consider system-specific dynamics when designing habitat manipulation projects to improve black bass reproduction. Physical features preferred in one system may not be available in another, and spawning adults may only respond to familiar habitat features. These physical features, particularly the physical structure within the littoral zone, affect the abundance and behavior of brood predators, and both habitat features and brood predators affect parental care. We also recommend that managers conduct in-water surveys of nesting fish prior to designing habitat manipulation projects whenever possible. Finally, we suggest that managers place supplemental structure strategically with respect to existing physical structure within the littoral zone. In particular, supplemental structure should not be placed too close to patches of complex structure.

Introduction

Fisheries managers and anglers want more black bass, and they want cost effective means of enhancing black bass populations. Conservation biologists strive to sustain populations of native fishes whether they are of interest to anglers or not, and their concerns extend to the rarer species of *Micropterus* basses. A key to both goals is producing more surviving offspring. Successful spawning must occur if black bass populations are to remain sustainable- whether they are harvested populations of ubiquitous species, or rare species in need of conservation.

Fisheries managers over the past few decades have sought to enhance spawning by manipulating littoral habitat, typically by adding physical structure to nearshore areas. These supplementation projects are based on early, general observations of black bass nesting (e.g., Carbine 1939, studies cited in Coble 1975 and Miller 1975), and on the assumption that "if we build it, they will come." In other words, if fisheries managers provide physical structure, individual males will seek the artificial reefs or brush piles or logs and then construct their nests nearby. Our goal here is to consider how ecological and behavioral aspects of black bass reproduction affect the success of attempts to enhance black bass spawning.

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Studies of the effects of supplemental physical structure on the distribution, growth, production, and angler harvest of *Micropterus* basses quantify and support the potential benefits of these efforts. For example, Vogele and Rainwater (1975) added brush shelters to the structurally-depauperate littoral zone of Bull Shoals Reservoir, Arkansas, attracting spawning largemouth bass *Micropterus salmoides* and spotted bass *M. punctulatus*. Hoff (1991) added half-log structures to five inland lakes in Wisconsin, dramatically increasing nest density, spawning success and recruitment of fingerlings of smallmouth bass *Micropterus dolomieu*. Other studies demonstrate similar positive effects following supplementation (e.g., Dufour 1991; Hunt and Annett, in press).

Ramifications of habitat manipulation projects are not universally positive, however, and even well-conceived projects may fail or even cause harm. For example, largemouth bass stocked into ponds containing brush piles experienced higher growth rates, but also increased vulnerability to angling, compared to largemouth bass in control ponds lacking artificial structure (Wege and Anderson 1979). While this vulnerabilities clearly benefits anglers, it is potentially harmful to parental black basses. Sometimes spawning individuals simply ignore supplemental structure, which results in valuable effort and resources being wasted. Obtaining information about unsuccessful habitat manipulation projects is difficult. Investigators rarely publish negative results, because they are difficult to publish and may not reflect favorably on the investigators. As a consequence, planning projects to avoid failure (or harm) becomes unnecessarily problematic.

How can well-intentioned, time- and resource-constrained fisheries professionals predict whether their projects will be successful or a waste of effort? We decided to use data from our research on the ecology and behavior of spawning largemouth bass to address this question. Our studies, conducted from 1991 through 1998, include surveys of nearly 650 nests constructed in three very different systems: a small Arkansas reservoir, research ponds in Kansas, and a kettlebasin lake in Michigan. This body of research includes studies of nest site selection, parental behavior, seasonal microhabitat use by juvenile centrarchids, habitat selection by nonnesting centrarchids during largemouth bass reproduction, and effectiveness of several habitat manipulation projects (Dibble 1993; Hunt 1995; Annett et al. 1996, Hunt, unpublished data). Here, we highlight broad patterns from several of these studies that are relevant to the potential success of habitat manipulation projects. We first review nest-site preferences of largemouth bass in each of these systems, noting both similarities and differences among the three populations. We then focus on the physical structure commonly associated with nests of largemouth bass, considering some of the behavioral phenomena of parental bass and brood predators that are associated with the presence and complexity of structure. Finally, we use these three lentic systems, and our own efforts at modifying spawning habitat, as case studies to examine why habitat manipulation may or may not be successful.

Study Sites

Lake Wedington, Arkansas

Lake Wedington is a small (41 ha) impoundment in the Illinois River watershed located in the Ozark National Forest near Fayetteville, Arkansas. Land use in the hilly watershed is primarily second growth deciduous forest with little agricultural development. Lake Wedington has a distinct littoral zone with substrates ranging from silt to boulder, but dominated by gravel and cobble. In most areas of the lake, the littoral zone slopes steeply. Naturally occurring physical structure, which includes logs, stumps, woody debris, aquatic macrophytes, and leaf packs, is abundant in the relatively narrow littoral zone (Annett et al. 1996). We searched for nests of largemouth bass throughout the various littoral habitats in the lake, including those representative of the variation in slope, substrata, and amount and types of physical structure (see below). Largemouth bass are abundant in Lake Wedington, as are bluegill *Lepomis macrochirus*, longear sunfish *Lepomis megalotis*, and redear sunfish *Lepomis microlophus*.

NESA Ponds, Kansas

We constructed four sites for nests in each of 12 small (surface area approximately 0.04 ha, mean depth 1.2 m) earthen ponds in the University of Kansas Nelson Ecological Study Area (NESA). Each nest site contained a 1.5 m × 1.5 m layer of gravel and one of the following: a log elevated by two concrete blocks; a submerged small conifer; both structures; no physical structure. The location of these four treatments was randomized among nest sites within each pond. During April and early May 1994, approximately 12 tagged largemouth bass were stocked into each pond, along with bluegill and green sunfish *Lepomis cyanellus*, and a variety of cyprinids.

Pine Lake, Michigan

Pine Lake is a shallow kettlebasin lake (mean surface area approximately 40 ha) located in the Manistee National Forest between Manistee and Cadillac, Michigan. The rolling topography of the watershed is of glacial origin; land use is primarily second growth forest composed of mixed hardwoods and conifers. Pine Lake has a gently sloping bathymetry, with a broad littoral zone dominated by sand and silt. Naturally occurring physical structure includes logs, branches, woody debris, and attached aquatic macrophytes. Our habitat surveys show that this physical structure is distributed unevenly among three concentric mesohabitats that compose the littoral zone: nearshore habitat, which contains relatively abundant woody debris and somewhat sparse aquatic macrophytes in a zone approximately 0–20 m offshore; open habitat, which contains only sparse, short aquatic macrophytes and very sparse woody debris approximately 20–60 m offshore; and offshore habitat, which contains relatively abundant, taller aquatic macrophytes and patches of woody debris located approximately 60–100 m offshore. We sampled each of these mesohabitats for nests of largemouth bass, searching littoral habitats adjacent to the northern, southeastern, and western shores of Pine Lake (see next section). Largemouth bass are abundant in the lake, as are bluegill, rock bass *Ambloplites rupestris*, yellow perch *Perca flavescens*, johnny darters *Etheostoma nigrum*, and a variety of cyprinid species.

Methods

Monitoring Nests and Potential Brood Predators

Largemouth bass were monitored while nesting during 1991, 1992, and 1993 in Lake Wedington (Arkansas; $N_{1991–1993}$ = 329 nests), during 1994 in the NESA ponds (Kansas; N = 18 nests), and during 1996, 1997, and 1998 in Pine Lake (Michigan; $N_{1996–1998}$ = 298 nests). To locate nests, which are visually distinct from undisturbed substratum, pairs of divers scanned the substratum of littoral habitat 0–3 m deep while swimming (nests were never found at depths > 2.8 m). Nests were surveyed in: littoral habitat adjacent to a total of 3,250 m of shoreline in Lake Wedington; each of the NESA ponds exhaustively; and littoral habitat adjacent to a total of 1,800 m of shoreline in Pine Lake. Divers confirmed the identity of the nesting species by observing the parental male whenever possible. Each nest was assigned a unique identification number marked by tags attached to sinkers, and the nest depth, brood presence and composition (embryos, yolk sac fry, or free swimming fry), substratum type, and category of physical structure located within 1 m of the nest perimeter were recorded (see below for categories of substrata and physical structure used). Littoral habitat was surveyed every two to four days for new nests and for the status of old nests until spawning was complete.

During 1997, the distribution and abundance of potential brood predators was assessed in Pine Lake by surveying 156 belt transects (2 m × 100 m) located at random within 10 m wide zones arrayed parallel to shore (i.e., one transect located at random 0–10 m offshore, one transect located 10–20 m offshore, etc., to a zone located 70–80 m offshore). Because early surveys indicated that many fish occupied habitat very near shore, transects located 0–2 m offshore were also surveyed. Potential brood predators were defined as all nonnesting fishes observed, including bluegill, rock bass, largemouth bass, yellow perch, and a variety of cyprinids. Transects were positioned within each 10 m wide zone at random. Fish in habitat located more than 80 m offshore were not sampled because water clarity in these areas was often insufficient for detecting and identifying small fish with accuracy. Divers used an anchored meter tape to measure distances and checksheets to note the species of each fish encountered within the belt transects as well as the category of physical structure located within 1 m of the fish (categories are defined below). Centrarchids were designated as juveniles or adults based on TL (i.e., relatively small individuals in each species were categorized as juveniles and relatively large individuals as adults). The reproductive status or specific age of individuals were not inferred by these designations; their size and potential as brood predators were of greatest relevance to this study. Underwater observation of fishes along transects is an efficient, accurate means of sampling centrarchids, other littoral species that associate with physical structure, and fish species that are relatively sessile (Dibble 1991; Annett et al. 1996; Dolloff et al. 1996).

Determining Habitat Availability

The abundance and distribution of physical structure and of different textures of substrata within the littoral zones of Lake Wedington (Arkansas) and Pine Lake (Michigan) were determined by sampling 100 m line transects arrayed parallel to shore. In Lake Wedington, 15 transects were sampled (total habitat surveyed = 1,500 m) located in representative areas of the littoral zone that were also surveyed for nests. Because the littoral zone in Pine Lake is exceptionally broad, habitat transects arrayed in 10 m intervals were surveyed (e.g., one transect located at random 0–10 m offshore, one located 10–20 m offshore, etc.). Habitats were sampled until the depth became too great to view features clearly on the lake bottom (total habitat surveyed = 9,600 m). For each transect, the linear distance of patches of different categories of substratum and physical structure were measured (defined below). Each patch was measured from the point where a category was first intercepted until the point at which it changed to a new category (Annett et al. 1996). Substrata and physical structure were measured simultaneously, but were recorded separately. From these data, we determined percent availability of each type of physical structure and substratum in the littoral zones of Lake Wedington and Pine Lake.

All types of physical structure associated with largemouth bass nests were combined into four categories designated by complexity (determined by the abundance and size of interstices; Johnson and Stein 1979; Johnson et al. 1988, Gotceitas and Colgan 1987; Gotceitas 1990), including: simple structure, defined as structure possessing few, large or wide interstices, such as logs, stumps, boulders, or the trunk of a submerged tree; complex structure, defined as structure possessing many, small or narrow interstices, such as patches of attached aquatic macrophytes, brush piles, large leaf packs, or the branched portion of submerged trees; simple and complex structure, which includes any combination from categories 1 and 2 above; none, which is the absence of notable physical structure within 1 m of the nest site. These four categories were selected because of the effect that structural complexity can have on the abundance and behavior of fish in aquatic ecosystems (Crowder and Cooper 1982, Gotceitas and Colgan 1987; Johnson et al. 1988, Heck and Crowder 1991; Hoff 1991; Weaver et al. 1996), including nesting largemouth bass and their brood predators. For example, bluegill and juvenile largemouth bass, which are predators of centrarchid fry, congregate in patches of complex structure in Lake Wedington (Dibble 1993; Annett et al. 1996).

Substrata were quantified visually during surveys using a modified Wentworth scale (Bovee 1982). These were subsequently simplified by combining different categories as follows: fine, which included all substrata dominated by silt; medium, which included all substrata dominated by sand or gravel, and also included nests whose embryos were attached to aquatic vegetation (roots, stems, or leaves); coarse, which included all substrata dominated by cobble or boulders; and continuous, which included any nest whose substratum was composed of a relatively continuous surface, such as embryos attached to the surface of a stump, a horizontal log, a boulder, or a sheet of clay.

Monitoring Behavior

We observed the behavior of parental largemouth bass and potential brood predators in Pine Lake during 1997. Parental behavior of 54 male largemouth bass was observed during 15 minute bouts of focal animal sampling (Lehner 1996). Nests of these parental males were distributed representatively throughout all three mesohabitats found within the littoral zone of Pine Lake. Observers used anchored floating mats to stabilize their position, minimizing disturbance to the parental male. After waiting until parental males resumed normal behavior, observers recorded all occurrences of parental aggression (e.g., displays, bites, chases) as well as the number, species, and age-class of all fish intruding into nest territories (defined as the area within a 2 m radius of the nest site). We also noted the category of physical structure associated with the nest and the mesohabitat (nearshore, open, or offshore) in which the nest was located.

Habitat Manipulation

Each of the systems studied contained structure added to the littoral zone expressly to benefit largemouth bass spawning. Lake Wedington contained 30 pressure-treated logs elevated by concrete blocks; these logs were installed in March 1992, and were removed after the reproductive season ended (Hunt and Annett, in press). The 12 NESA ponds contained a total of 24 pressure-treated logs and 24 small, submerged conifers placed adjacent to nest sites constructed with gravel substratum. Twelve logs and 12 conifers were placed in isolation, the remaining 12 logs and conifers were placed in sets near nest sites (see study sites for additional detail). Pine Lake contained tree drops in three large sections of littoral habitat (each > 100 m in length) located adjacent to the northern, southeastern, and western shorelines. The tree drops remained in place during all three years of study in Pine Lake. Lake Wedington and Pine Lake had areas of unmanipulated habitat that served as controls. Largemouth bass nests were monitored with respect to these manipulations in each of the three systems. Details of the Lake Wedington and Pine Lake experiments will not be reported here, but the overall effectiveness of all three habitat manipulation projects will be discussed in relation to nest site selection and behavior of parental largemouth bass and brood predators.

Data Analysis

Mean nest depth was compared among the seven years of study, among the three years of study in Lake Wedington, and with the three years of study in Pine Lake using one-way analysis of variance (ANOVA; Sokal and Rohlf 1995). Preferences of nesting largemouth bass and of potential brood predators were determined among different types of physical structure, substrata, and mesohabitat using Manly Selectivity Indices (Manly 1974), comparing availability of each type of physical structure, substratum, or mesohabitat to its use by nesting largemouth bass or potential brood predators. Manly selectivity values were tested for significance using x^2 Goodness-of-fit Tests (Manly 1974; Sokal and Rohlf 1995).

Rates of intrusion by potential brood predators (nonnesting fish) towards nests associated with different categories of physical structure were copared using one-way ANOVA. Rates of parental aggression by parental largemouth bass were compared among different categories of physical structure using one-way ANOVA (Sokal and Rohlf 1995). For these tests, different types of physical structure were combined into three categories: simple structure only; complex structure with or without simple structure; and no structure. The relationship between parental aggression and rates of intrusion toward nests was examined with linear regression (Dunn and Clark 1987).

To compare the effectiveness of habitat manipulation projects among the three systems, numbers of nests constructed near supplemental structure we compared to the numbers of nests constructed elsewhere in manipulated habitats (near naturally occurring structure, or on sites lacking physical structure) using a x^2 Contingency Test (Siegel 1956). For this analysis, we considered only nests constructed in manipulated habitat (i.e., supplemented areas of Lake Wedington during 1992, all NESA ponds during 1994, and supplemented areas of Pine Lake during 1996–1998).

Results

Largemouth Bass Nests

During these studies 645 nests were observed, 329 in Lake Wedington, 18 in the NESA ponds, and 298 in Pine Lake. Spawning males constructed their nests within a relatively narrow range of depths. Nest depth ranged from 0.1 to 2.8 m, with a mean of 1.3 m for all three systems (Table 1). Mean depth varied significantly from year to year, ranging from 0.6 m in the NESA ponds during 1994, to 1.6 m in Pine Lake during 1997 (one-way ANOVA; $P < 0.005$; Table 2). Differences in annual mean depth also varied significantly among years within Lake Wedington (one-way ANOVA; $P < 0.005$; Table 2) and Pine Lake (one-way ANOVA; $P < 0.005$; Table 2).

Spawning males frequently used substrata of medium texture for their nests (Figure 1). Of all nests surveyed, 76.7 percent had sand or gravel-

Table 1. Number of nests and mean depth of nests surveyed in Lake Wedington, Arkansas (LW), 12 ponds in the Nelson Ecological Study Area, University of Kansas, Kansas (NESA), and Pine Lake, Michigan (PL).

Year of study and system	Number of nests	Mean depth (m ± SE)	Range of depths (m)
1991 LW	127	1.18 ± 0.0451	0.1–2.6
1992 LW	139	1.25 ± 0.0425	0.2–2.4
1993 LW	63	1.50 ± 0.0506	0.5–2.4
1994 NESA	18	0.60 ± 0.0415	0.2–1.2
1996 PL	111	1.30 ± 0.0328	0.4–2.5
1997 PL	101	1.60 ± 0.0477	0.5–2.6
1998 PL	86	1.44 ± 0.0606	0.1–2.8
Total	645	1.30 ± 0.0419	0.1–2.8

Table 2. Analysis of variance for depth of largemouth bass nests surveyed in Lake Wedington, Arkansas ($N_{1991} = 127$; $N_{1992} = 139$; $N_{1993} = 63$), ponds in the Nelson Ecological Study Area, University of Kansas, Kansas ($N_{1994} = 18$), and Pine Lake, Michigan ($N_{1996} = 111$; $N_{1997} = 101$; $N_{1998} = 86$).

Source of variation	Sum of squares	df	Mean square	*F* ratio
All systems (1991–1998)				
Among years	19.8645	6	3.3107	16.1576***
Within years	130.7262	638	0.2049	
Lake Wedington (1991–1993)				
Among years	4.0678	2	2.0339	9.36348***
Within years	68.8186	326	0.2111	
Pine Lake (1996–1998)				
Among years	4.5354	2	2.2677	10.9976***
Within years	60.8290	295	0.2062	

***$p < 0.005$

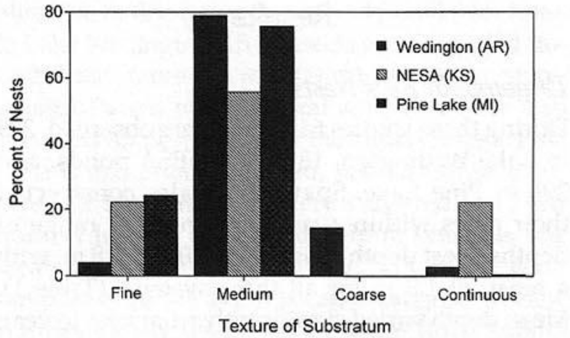

Figure 1. Percent of largemouth bass nests associated with substrata of fine, medium, coarse, and continuous texture in Lake Wedington, Arkansas ($N = 329$), in 12 ponds in the Nelson Ecological Study Area, Kansas ($N = 18$), and in Pine Lake, Michigan ($N = 298$). See text for definitions of categories used.

dominated substrata. Relatively few nests were constructed on fine or very coarse substrata (21% for both categories combined), even though fine substrata were common in both Pine Lake and the NESA ponds, and coarse substrata were common in Lake Wedington. Coarse substrata were not observed in Pine Lake. A few nests (2.3%) were found on relatively continuous, but rare, substrata such as the tops of stumps, logs, large boulders, or clay slabs. In both Lake Wedington and Pine Lake, nesting largemouth bass showed significant preferences for substrata of medium texture, and significant avoidance of substrata of fine texture; nesting males avoided coarse substrata in Lake Wedington (Manly Selectivity Indices and x^2 Goodness-of-fit Tests, $x^2_{Wed} = 600.11$, df = 3, $P < 0.005$; $x^2_{PL} = 160.27$, df = 2, $P < 0.005$; Figure 2).

Most spawning males nested near physical structure; only 14.9 percent of nests surveyed in all three systems lacked physical structure. More than half of all nests were located near large, simple woody structure, either alone or in combination with complex physical structure. Complex structure was much more abundant than simple structure in both systems, and a large number of nests were found near complex structure (Figure 3). Largemouth bass strongly preferred nesting near simple structure in both Lake Wedington and Pine Lake and avoided sites without some type of physical structure nearby; parental males displayed weak preference for complex structure in Lake Wedington and used complex structure proportionally to its availability in Pine Lake (Manly Selectivity Indices and x^2 Goodness-of-fit tests; $x^2_{Wed} = 223.91$, df = 3, $P < 0.005$; $x^2_{PL} = 115.3$, df = 3, $P < 0.005$; Figure 4).

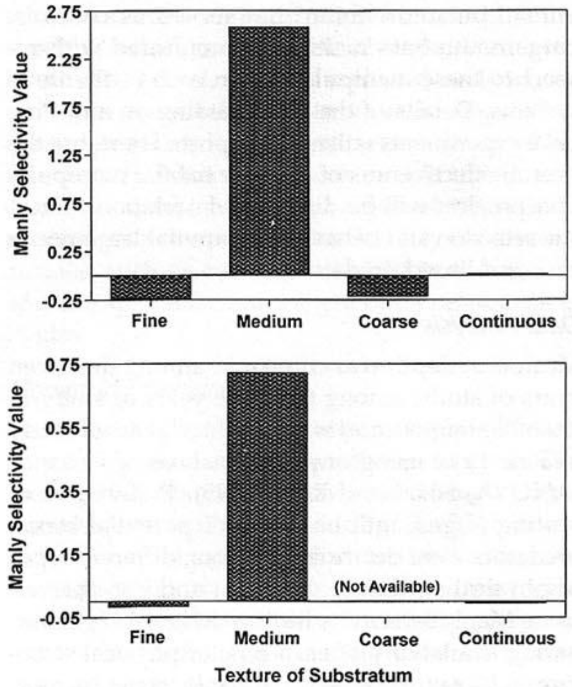

Figure 2. Manly selectivity indices for largemouth bass nesting in association with substrata of fine, medium, coarse, and continuous texture in Lake Wedington, Arkansas (top panel), and Pine Lake, Michigan (bottom panel). Positive values indicate behavioral preference; negative values indicate behavioral avoidance (note that negative values are constrained mathematically and cannot be less than –0.25; positive values are not constrained).

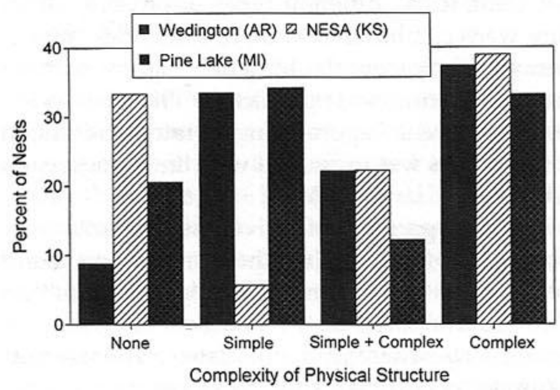

Figure 3. Percent of largemouth bass nests associated with different categories of physical structure in Lake Wedington, Arkansas ($N = 329$ nests), 12 ponds in the Nelson Ecological Study Area, Kansas ($N = 18$ nests), and Pine Lake, Michigan ($N = 298$ nests). See text for definitions used for categories of complexity of physical structure.

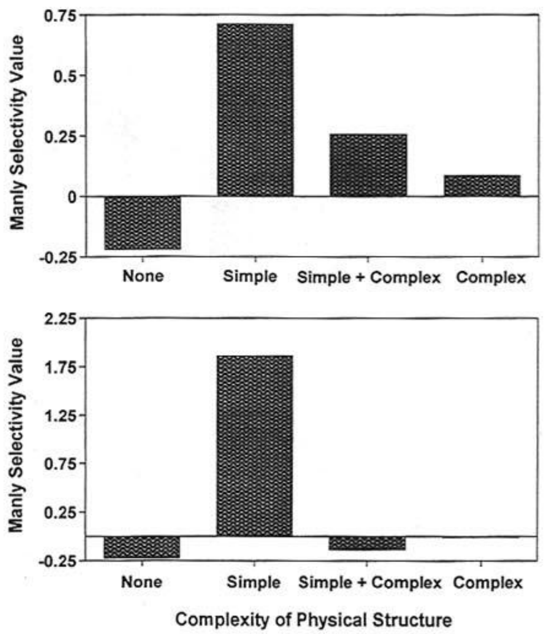

Figure 4. Manly selectivity indices for largemouth bass nesting in association with different categories of physical structure in Lake Wedington, Arkansas (top panel), and Pine Lake, Michigan (bottom panel). Positive values indicate behavioral preference; negative values indicate behavioral avoidance. Negative values are constrained mathematically and cannot be less than –0.25; positive values are not constrained.

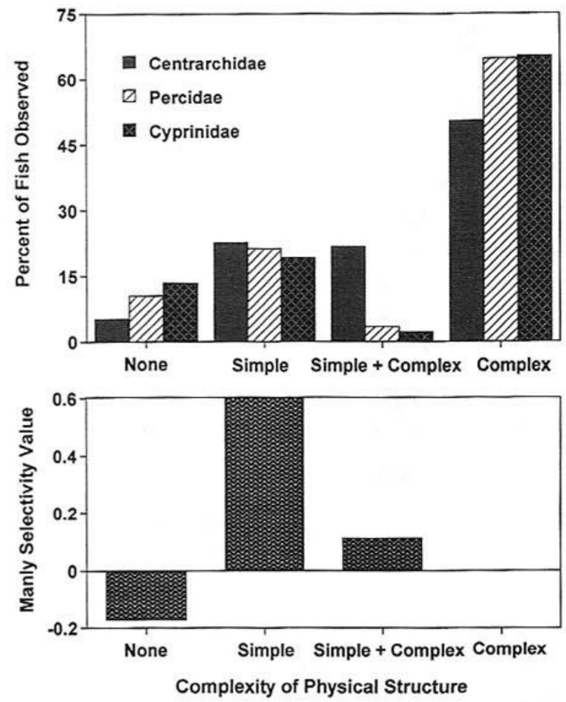

Figure 5. Top panel: percent of nonnesting fishes belonging to the families Centrarchidae (N = 1,512), Percidae (N = 803), and Cyprinidae (N = 2,773) associated with different categories of physical structure in Pine Lake, Michigan during 1997. Bottom panel: Manly selectivity indices for nonnesting fish (N = 5,088) observed in association with different categories of physical structure in Pine Lake, Michigan. Positive values indicate behavioral preference; negative values indicate behavioral avoidance (note that negative values are constrained mathematically and cannot be less than –0.25; positive values are not constrained). See text for definitions used for categories of complexity of physical structure.

Potential Brood Predators (Nonnesting Fish)

During 1997 we surveyed 5,088 nonnesting fish, including 2,773 cyprinids, 803 percids, and 1,512 centrarchids. Of these fish, 89.5 percent were associated with some type of physical structure (Figure 5). Generally, only adult largemouth bass, johnny darters, and, very occasionally, rock bass were observed in exposed areas lacking physical structure, and only johnny darters behaved as if they were residential rather than transient (i.e., were not swimming rapidly when first observed; in comparison, most fish observed in patches of physical structure were relatively immobile). Most nonnesting fish (67.8%) were observed in association with complex physical structure. Like nesting largemouth bass, potential brood predators avoided habitat lacking physical structure and preferred habitat containing simple structure, with or without complex physical structure; they used patches of complex structure proportionally to its availability (Manly Selectivity Indices and x^2 Goodness-of-fit test, $x^2 = 469.3$, df = 3, $P < 0.005$; Figure 5).

Most potential brood predators were observed in nearshore mesohabitat, typically less than 3 m offshore (e.g., 97.2% of juvenile centrarchids; Figure 6). In contrast, most largemouth bass nested at least 30 m offshore (40.6% in open mesohabitat and 49% in offshore mesohabitat; Figure 6). Nonnesting fish exhibited strong preference for nearshore mesohabitat and strong avoidance of open and offshore mesohabitat (Manly Selectivity Indices and x^2 Goodness-of-fit Test, $x^2 = 4{,}055.8$, df = 2, $P < 0.005$; Figure 6). Spawning largemouth bass exhibited exactly the opposite pattern, avoiding nearshore mesohabitat and preferring open and offshore mesohabitat (Manly Selectivity Indices and x^2 Goodness-of-fit Test, $x^2 = 8.04$, df = 2, $P < 0.05$; Figure 6).

Behavior

Rates of intrusion by potential brood predators into nest territories (the area immediately around nest sites) and rates of parental aggression both in-

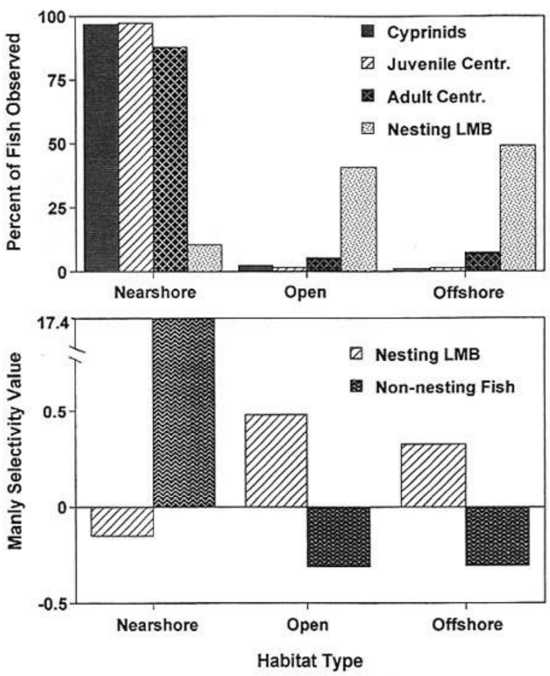

Figure 6. Top panel: percent of cyprinids ($N = 2,773$), juvenile centrarchids ($N = 1,113$), nonnesting adult centrarchids ($N = 399$), and nesting largemouth bass ($N = 101$) associated with different nearshore, open and offshore mesohabitats in Pine Lake, Michigan, during 1997. Bottom panel: Manly selectivity indices for cyprinids, juvenile centrarchids, nonnesting adult centrarchids, and nesting largemouth bass associated with different mesohabitats in Pine Lake during 1997. Positive values indicate behavioral preference; negative values indicate behavioral avoidance. Negative values are constrained mathematically and cannot be less than –0.3333; positive values are not constrained. See text for definitions of littoral mesohabitats.

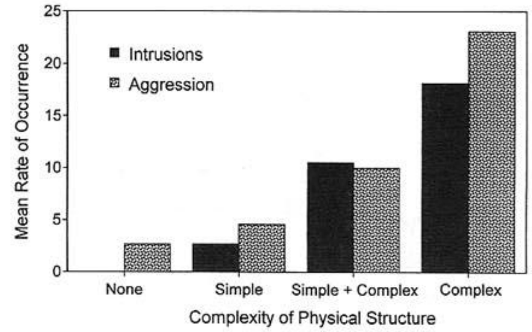

Figure 7. Mean rate (N/hour) of intrusions by nonnesting fish into territories of nesting largemouth bass, and mean rate (N/hour) of aggressive behaviors by parental largemouth bass in Pine Lake, Michigan, during 1997. Mean rates of intrusion and aggression are shown in association with different categories of physical structure.

creased as the complexity of physical structure associated with nests increased (Figure 7). Parental males guarding nests associated with complex structure experienced rates of intrusion four to seven times higher than those experienced by males guarding nests associated with simple structure (Figure 7). The rate of intrusion by brood predators into nest territories was significantly higher for nests located near complex structure compared to those located near simple structure or those lacking structure (one-way ANOVA; $P < 0.05$; Table 3). Parental males displayed significantly higher rates of aggression when nesting near complex structure than when nesting near simple structure alone or when nesting without any nearby physical structure (one-way ANOVA; $P < 0.01$; Table 4).

Parental aggression increased significantly as rates of intrusion by potential brood predators increased (linear regression, $N = 54$, $r^2 = 0.673$, $F = 107.25$, $P < 0.005$; Figure 8).

Habitat manipulation projects

Although more than 85 percent of parental males nested near physical structure, often this was not the structure provided for them in the habitat enhancement projects. Only 28 of 202 (13.9%) largemouth bass nests found in manipulated habitat were located near the supplemental structure we provided. Success of habitat manipulation projects, however, did vary among systems. Largemouth bass nested readily in association with the supplemental logs placed in Lake Wedington, even though naturally occurring woody structure is relatively abundant there. Spawning males constructed nests in association with 20 of the logs added to Lake Wedington (66.7% use of supplemental logs), com-

Table 3. Analysis of variance for rate of intrusion of potential brood predators into territories of largemouth bass nesting in association with simple structure (SS), complex structure (CS), or no structure (none). Behavior of potential brood predators was observed in Pine Lake, Michigan, during June, 1997 ($N_{SS} = 21$; $N_{CS} = 22$; $N_{None} = 11$).

Source of variation	Sum of squares	df	Mean square	F
Among categories of structure	141.3070	2	70.6535	3.3202*
Within categories of structure	1,085.2800	51	21.2800	

*$p < 0.05$

Table 4. Analysis of variance for rate of parental aggression of largemouth bass nesting in association with simple structure (SS), complex structure (CS), or no structure (none). Behavior of parental largemouth bass was observed in Pine Lake, Michigan, during June, 1997 ($N_{SS} = 21$; $N_{CS} = 22$; $N_{None} = 11$).

Source of variation	Sum of squares	df	Mean square	F
Among categories of structure	156.3022	2	78.1511	6.0461*
Within categories of structure	659.2209	51	12.9259	

*$p < 0.01$

prising 64.5 percent of all nests constructed in the manipulated habitat. In contrast, the supplemental structure added to the NESA ponds and to Pine Lake was largely ignored. Only one nest was constructed near the logs in the NESA ponds (4.2% use of supplemental logs and 5.6% of all nests constructed), even though the ponds contained very little naturally occurring physical structure and the logs used were identical to those added to Lake Wedington. Supplementation was not any more effective in Pine Lake. Spawning males constructed only seven nests near the tree drops (4.6% of all nests constructed in manipulated habitat). The differences between the relatively high use of supplemental logs in Lake Wedington and the infrequent use of supplemental structure in the NESA ponds and in Pine Lake were highly significant (x^2 Contingency test; $x^2 = 78.64$; df = 2; $P < 0.005$).

Discussion

Our behavioral observations in Lake Wedington (Hunt 1995) and Pine Lake (current study) provide strong evidence that parental behavior differs between males that nest near simple structure and those that nest near complex physical structure. Although fisheries biologists have contemplated

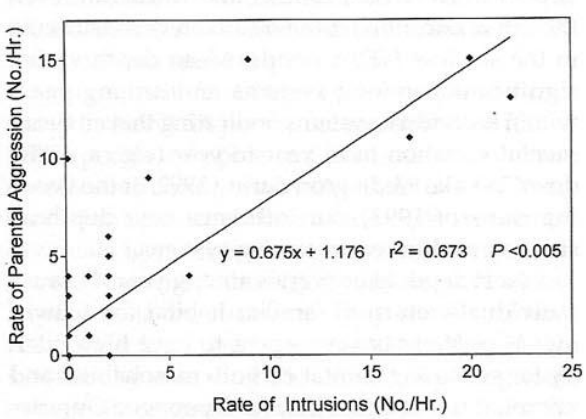

Figure 8. Rate of parental aggression displayed by nesting male largemouth bass in comparison to the rate of intrusions by nonnesting fish into their nest territories. Behavior was observed in Pine Lake, Michigan, during 1997.

the potential benefits to parental males of nesting near physical structure (e.g., protection from avian predators, provision of shade to enhance vision; Helfman 1981), the behavioral effects of nesting near different types of physical structure have received little attention. We found that parental males are more aggressive when nesting near complex structure, largely because they face intrusion by more potential brood predators compared to individuals that nest near simple structure or in areas without structure. Ultimately, largemouth bass nesting near complex structure face higher rates of brood predation. Juvenile sunfish and cyprinids, which are themselves vulnerable to predation, occur in higher densities in patches of complex structure because they use the patches as refugia from piscivorous predators (Gotceitas and Colgan 1987, Savino and Stein 1989; Gotceitas 1990, Gotceitas and Colgan 1990). Brood predators also use complex structure to hide from guarding parents, allowing them to approach more closely to the brood before detection by the parent (Annett 1998; Annett et al. 1999). The higher density of brood predators coupled with their increased effectiveness makes it risky for parental males to nest near complex physical structure.

Increased attention to intruders is also costly to parents and their offspring. Chases and other highly aggressive behaviors are energetically expensive, and intruders draw parental males away from their nest sites (Colgan and Brown 1988, Hinch and Collins 1991; Sabat 1994; Hunt 1995, current study). Unprotected broods are highly vulnerable to predators and may be decimated quickly (Eipper 1975, Hinch and Collins 1991; Kieffer et al. 1995, Steinhart et al. 2000). Parental males exposed to repeated attacks by brood predators spend less time hovering above their broods, a position from which they can both fan developing embryos and effectively deter predation (Eipper 1975, Bain and Helfrich 1983, Colgan and Brown 1988, Coleman and Fischer 1991, Ongarato and Snucins 1993; Hunt 1995, Steinhart et al. 2000).

On the opposite extreme, nest sites that lack physical structure may also cause problems for parents and their broods. Parental males experience few intrusions and display little parental aggression when nesting without physical structure, but they also lack protective cover. Nest sites are swept clean of debris and differ visibly in color and other aspects from the surrounding substratum. Males nesting without cover become visual targets while hovering over their broods, which can make them vulnerable to avian predators (and anglers) that attack from above. Our casual observations in all three systems indicate that males nesting without structure often hover above the darker substratum adjacent to nest sites, where they become relatively cryptic, rather than above the broods themselves. These parental males also tend to be skittish, often swimming away from nest sites in response to minor disturbances. Broods in such nests may thereby receive less fanning and protection from parental males. We did not quantify data that address these concerns, but suggest that investigation of the relationships between physical structure, visual conspicuousness, parental tenacity and vulnerability to avian (and angler) attack is warranted.

Management Implications

Spawning largemouth bass throughout their natural distribution and among strikingly different lentic systems demonstrate consistent preferences for three habitat features: physical structure, substratum, and depth (Kramer and Smith 1962; Miller 1975; Bruno and Gregory 1990; Annett et al. 1996, current study). Smallmouth bass also exhibit preferences among the physical structure, substrata, and depths available to them (Coble 1975; Vogele 1981; Goff 1986; Ridgway et al. 1991), and we can reasonably assume that other *Micropterus* basses are equally choosy about the microhabitat in which they spawn (Miller 1975). Awareness of these preferences is a good first step in providing resources that foster spawning in largemouth bass and other *Micropterus* basses.

Physical structure remains the focus of most supplementation projects, and our extensive data confirm the strong preference that largemouth bass have for spawning near cover, particularly simple, woody structure. Although many individuals nest near complex physical structure, selectivity indices indicate that they resort to such associations because of their ubiquitous, strong avoidance of nesting in exposed sites lacking any structure (Figure 4; Annett et al. 1996); the relative abundance of aquatic macrophytes, woody debris, and leaf packs; and the rarity of logs, stumps, large branches and submerged trees. Woody structure typically composes less than 20 percent of littoral habitat in systems like Lake Wedington, where it is relatively abundant, and as little as less than one percent of littoral habitat in systems like Pine Lake, where it is scarce. Nesting males nest near complex physical structure because it is relatively abundant, not because it is preferred; Manly Selectivity Indices in Lake Wedington and Pine Lake indicated only a weak preference for, or even weak avoidance of, these structural patches (Figure 4; Annett et al. 1996).

The specific texture of nest substratum varies from system to system depending on availability, but spawning largemouth bass in all three systems we studied sought microhabitat dominated by sand or gravel. Where sediments dominated by sand or gravel are not available, it may not benefit spawning fish if managers attempt to provide it. Our work in the NESA ponds suggests that providing patches of gravel or other appropriate substratum will not attract spawning males if the material is unfamiliar to them. The individuals we stocked, collected from local reservoirs and large ponds, sought the types of stable substrata familiar to them- which did not include gravel. In systems dominated by silty or unstable substrata, such as many lentic systems in Kansas, largemouth bass will spawn directly on the roots, rhizomes, or stems and leaves of attached aquatic macrophytes (Carbine 1939; Kramer and Smith 1962; Allan and Romero 1975; Bruno and Gregory 1990; NESA, experiment of current study). When necessary, males will spawn on clay slabs, bedrock, rubble, boulders, stumps, and even the horizontal surfaces of submerged logs (Miller and Kramer 1971; Allan and Romero 1975; Hunt 1995; current study).

Nests were found in nearly identical ranges of depths in Arkansas, Kansas and Michigan, even though maximum depth was severely constrained in the shallow NESA ponds. Mean depth varied significantly among systems and among years within individual systems, indicating that environmental variation from year to year (e.g., a drawdown in Lake Wedington during 1992, or the flooding rains of 1993) can influence nest depth as strongly as differences among systems.

Nest depth likely varies among years because individuals return to familiar habitat for spawning. *Micropterus* basses appear to have high fidelity for spawning habitat on both mesohabitat and microhabitat scales. In Lake Opeongo, Ontario, Canada, a system much larger than Lake Wedington or Pine Lake, smallmouth bass array their nests in patchy aggregates (Ridgway et al. 1991; Rejwan et al. 1997). Individual males tend to nest within 20 m of their previous year's nest site, and some males re-use the same nest site (Ridgway et al. 1991). In Pine Lake, at least 30 percent of males nested within 2 m of sites used the previous year (Hunt, unpublished data). Managers should note the tendency of spawning fish to use particular mesohabitat, and even specific nest sites within that habitat, again and again. It is important, therefore, to determine precisely where nests already occur before expending resources to manipulate habitat.

Habitat manipulation was relatively successful in Lake Wedington and relatively unsuccessful in the NESA ponds and in Pine Lake. Considering the location of nests in unmanipulated habitat and the types of physical structure and substrata naturally available to largemouth bass in these three systems, we can better understand why habitat manipulation was sometimes successful and sometimes not. When spawning individuals were familiar with the type of structure used for supplementation (i.e., we provided appropriate microhabitat), and when we placed this structure in areas of the littoral zone normally used for spawning (i.e., we manipulated appropriate mesohabitat), habitat manipulation was successful. When only one of these factors were considered, the efforts were unsuccessful.

Lake Wedington has a narrow, steep littoral zone (Dibble 1993) and relatively abundant woody structure that includes logs, stumps, branches, and felled trees. Nests are located in a narrow band of littoral habitat, rarely farther than 5 m offshore, because depths quickly exceed 3 m farther offshore (Hunt 1995). Largemouth bass in Lake Wedington routinely encounter woody structure located less than 5 m offshore, and the supplemental logs were placed in this same mesohabitat. Thus, physical structure similar to that naturally available was provided, and placed in the mesohabitat normally used for their spawning.

In contrast, familiar microhabitat was not provided in the NESA ponds. Largemouth bass for the NESA ponds were obtained from shallow, silty reservoirs and ponds containing little woody structure (Hunt, personal observation). The stocked individuals ignored the nest sites constructed with gravel, logs and submerged conifers, and nested instead near the shoreline. They sought suitable nest sites where and how they did in their native systems: by removing the silt and exposing roots of vegetation growing in the extreme shallows. We provided them with excellent resources, but resources with which they were unfamiliar.

We predicted that the tree drops in Pine Lake would attract spawning largemouth bass. Although parental males did spawn near logs and branches similar to the structure provided by the tree drops (Figure 3), very few spawned in association with the tree drops themselves. Our predictions were incorrect, largely because we did not anticipate the existence or importance of the three mesohabitats (nearshore, open, and offshore) revealed by our habitat surveys. The tree drops were located in nearshore mesohabitat less than 15 m offshore, but nearly 90 percent of nests were found in the open and offshore mesohabitats located more than 20 m from shore (Figure 6). A few nests were even found more than 100 m offshore, and more than 80 m away from the tree drops.

Our observations of parental largemouth bass and nonnesting fishes clarify why mesohabitat is so important in Pine Lake, with its broad, shallow littoral zone. Largemouth bass that spawn in Pine Lake have several mesohabitat options available to them, and through nest site selection they partition the littoral zone with nonnesting fishes (Figure 6). The tree drops are located in mesohabitat with high densities of potential brood predators. By nesting instead in open and offshore mesohabitat, parental males avoid encountering most potential brood predators (Figure 6).

Reflecting on our studies and those of others, we conclude that managers seeking to enhance spawning of *Micropterus* basses by manipulating littoral habitat may do so effectively by supplementing spawning habitat with simple woody structure like logs. When carefully placed, supplemental woody structure can attract nesting males and enhance nest density, numbers of successful nests, and recruitment of fingerlings (Vogele and Rainwater 1975; Hoff 1991; Dufour 1991, Hunt 1995, current study). This is particularly true in systems where woody structure is present naturally, but our anecdotal observations suggest that supplemental woody structure may eventually be accepted even where it is lacking naturally. Logs placed in a single 1 ha pond in NESA were ignored the first year, but attracted spawning largemouth bass during the second year of residence and each year thereafter (Hunt, unpublished data). Poor placement of structure was not overcome by familiarity in Pine Lake, however, which reinforces the idea that placement must account for the behavioral needs of nesting males.

Our work in Lake Wedington, much of which is not reported here, leads us to make several additional recommendations. First, we recommend that managers install structural units at least 7–10 m apart, spacing them about as far apart as the average inter-nest distance observed in the system of interest. Nesting *Micropterus* basses are solitary and territorial, so mimicking the local spacing of nests helps maximize use of the supplemental structure, as we achieved in Lake Wedington by spacing logs 7 m apart.

The proximity of complex physical structure to supplemental structural units is also important. Reproductive males may spawn in association with logs placed near complex structure, but they will likely suffer high rates of intrusion by brood predators if patches of complex structure are in close proximity, as we observed in Pine Lake. On the other hand, placing logs 5–10 m away from patches of complex structure may benefit bass fry. In Lake Wedington, fry schools still under parental care were most frequently observed in or near patches of physical structure located within 5 m of nest sites (Annett et al. 1996). We observed fry forming unstable aggregates after leaving the care of parental males in all three systems studied. These aggregates frequently stationed themselves near or within the interstices of patches of complex physical structure (Annett et al. 1996; Hunt, unpublished data). Thus, patches of complex structure located a moderate distance from nest sites serve as refugia for fry, and later, fingerlings (Dibble 1993).

Habitat selection is shaped by experiences in the particular environment in which an individual lives (Partridge 1978, Krebs and Davies 1984; Alcock 1998). Largemouth bass exhibit consistent preferences for their nest sites, but these preferences are tempered by experience. Features that are familiar are selected, while those that are not are ignored. For spawning largemouth bass, habitat that eschews brood predators is occupied; that which is filled with brood predators is avoided. The trends we observed in nest-site selection may differ from those of other populations in subtle, but important, ways. Understanding the behavioral and ecological dynamics unique to each population, as well as those universal to all populations, will foster better management and conservation of *Micropterus* basses.

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