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Variable Effects of Habitat Enhancement Structures across Species and Habitats in Michigan Reservoirs

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Abstract.—The addition of habitat enhancement structures to aquatic systems is a common practice by fisheries managers hoping to increase production, spawning success, and angler catch rates of important sport fishes. However, quantitative evaluations of these efforts are few and typically do not include the extent to which natural habitat mediates the effects of habitat enhancement structures. We evaluated the effects of two types of habitat enhancement structure on four fish groups in four reservoirs of the Au Sable River, Michigan. Using a combination of sampling methods, we compared several response variables (including relative abundance, nesting, and angler catch rates) between areas with and without structures, as well as before and after structure placement, across a gradient of natural habitat conditions. The effects of half-log habitat enhancement structures were significant in some cases, but no significant effects were detected for AquaCrib structures. Smallmouth bass *Micropterus dolomieu* responded to half-logs with significantly greater relative abundance, nest density, and nest success than in areas without half-logs. Other fish groups displayed few significant differences in the response variables between areas with and without structures or before and after structure placement. Habitat effects varied across reservoirs and fish groups but generally influenced the response variables more than the presence of habitat enhancement structures.

Fisheries managers have long recognized the potential of habitat enhancement structures to attract and hold fish (Brown 1986). The first state management agency to document the use of habitat enhancement structures was the Michigan Conservation Department, which added brush shelters and gravel piles to lakes in the early 1930s (Hazzard 1937). Since that time, numerous state and federal agencies and local organizations have undertaken habitat enhancement projects in both freshwater and marine systems using a variety of materials (Tugend et al. 2002). Habitat enhancement structures are added to aquatic systems when natural habitat is perceived to be lacking or insufficient (Prince et al. 1977), with the goal of providing additional cover and concentrating fish and so increasing some combination of recruitment, survival, growth, and angler catch rates (Johnson and Stein 1979).

Habitat enhancement structures can produce these positive effects through a variety of mechanisms. For example, habitat enhancement structures have been proposed to increase recruitment by providing cover for spawning (Vogele and Rainwater 1975; Hoff 1991; Hunt et al. 2002), thereby increasing nest density. Nest success may also increase if structures provide habitat that allows adults to more effectively protect their young (Hoff 1991). Structures can also offer refuge from predation and alter survival by increasing cover (Bohnsack and Sutherland 1985; Johnson et al. 1988; Moring and Nicholson 1994), providing shade (Helfman 1979, 1981; Johnson and Lynch 1992), and providing sites for orientation and schooling (Klima and Wickham 1971; Bohnsack and Sutherland 1985). Accordingly, prey abundance in the vicinity of structures may be enhanced (Wege and Anderson 1979; Aadland 1982; Moring et al. 1989), in turn increasing the abundance, feeding efficiency, and growth of predators (Wege and Anderson 1979; Bohnsack 1989). Habitat enhancement structures, particularly in the form of artificial reefs, also have been proposed to increase public access by making it easier for anglers to locate fish and to increase angler catch rates by concentrating fish (Bohnsack 1989).

Numerous studies have demonstrated that habitat enhancement structures succeed in concentrating fish in natural lakes (Wilbur 1974; Moring and Nicholson 1994) and reservoirs (Prince and Maughan 1979a; Brown 1986; Moring et al. 1989; Rogers and Bergersen 1999). However, the degree of concentration varies for several reasons, including the species present (Hubbs and Eschmeyer

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1938; Rodeheffer 1939, 1945), diel fluctuations in fish distribution (Moring and Nicholson 1994), the age of the structure (Wilbur 1978; Moring and Nicholson 1994), and the structure's physical attributes. In general, the average number of individuals and species attracted increases with the structural complexity achieved by increasing the volume, size, and surface area of habitat enhancement structures (Wickham et al. 1973; Rountree 1989; Graham 1992). Further, fish abundance varies with structure interstice size (the space within structures) in a complex fashion (Wege and Anderson 1979; Johnson et al. 1988; Lynch and Johnson 1989; Walters et al. 1991).

The morphometric characteristics of lakes and reservoirs in which habitat enhancement structures are installed also influence their effectiveness. Habitat enhancement structures may be relatively ineffective in systems with bathymetrically complex bottoms (Pardue and Nielsen 1979) or alternative natural habitat (Wilbur 1978; Mitzner 1981; Madejczyk et al. 1998; Rogers and Bergersen 1999). The depth at which habitat enhancement structures are placed also influences structure use and is often dependent on the foraging and habitat preferences of resident species (Kayle 1986; Walters et al. 1991; Johnson and Lynch 1992). Reservoirs, in particular, are often targeted for habitat enhancement projects. Reservoir systems often lack natural habitat due to the removal of standing timber before or after flooding as well as the decay of timber, rapid siltation of rocky reefs and other firm substrate in littoral areas, or lack of aquatic vegetation caused by fluctuating water levels (Prince and Maughan 1978).

Before habitat enhancement structures can be used as a management tool to increase recruitment, survival, growth, and angler catch rates, fisheries managers must know the extent to which such structures concentrate fish. Then, by identifying the conditions under which habitat enhancement structures are most effective, fisheries managers can most successfully and economically use structures as a tool for increasing the reproduction, survival, growth, and angler catch rates of sport fishes in systems with insufficient natural habitat (Johnson and Stein 1979). Within this context, we evaluated two types of structure, half-logs and AquaCribs, in four reservoirs of the Au Sable River, Michigan. We used a combination of two approaches to do so: (1) comparison within reservoirs between similar areas with and without added structures and (2) comparison within a reservoir before and after the placement of structures. To determine the effectiveness of habitat enhancement structures at concentrating fish, we quantified the effects of structures on both relative abundance and angler catch rates of prevalent sport fishes. Substrate and the abundance of aquatic macrophytes and coarse woody material in these reservoirs varied, allowing us to evaluate the effectiveness of the structures across a gradient of natural habitat. We also sought to characterize the response of smallmouth bass *Micropterus dolomieu* to structures by evaluating nest density and nest success in addition to relative abundance and angler catch rates. Smallmouth bass were the most abundant piscivore in our study reservoirs, and previous studies have demonstrated that this species can benefit from habitat enhancement structures (Hoff 1991; Patrick 1996).

We predicted that areas with habitat enhancement structures would have higher fish density, greater angler catch rates, and increased nest density and nest success of smallmouth bass than areas without structures. In addition, we expected the magnitude of response to increase with decreasing percent cover of coarse woody material and aquatic macrophytes. Finally, we sought to develop management recommendations for the placement of habitat enhancement structures so that future such endeavors will be the most beneficial and cost effective.

Methods

Study Reservoirs

Consumer's Energy Company created six reservoirs on the Au Sable River, Michigan (Figure 1), between 1911 and 1924, four of which were included in this study. In general, the reservoirs are mesotrophic in nature with short retention times ranging from 1 to 12 d. Two of the reservoirs are operated to simulate run-of-river flow (Alcona and Foote ponds), while the other two (Loud and Cooke ponds) are peaking operations with daily water level fluctuations reaching 0.49 and 0.30 m, respectively (Kinney et al. 2001). Turbidities are moderate and generally decrease from the upstream to the downstream reservoirs (Table 1). The fish community in the reservoirs primarily consists of coolwater and warmwater fishes, some coldwater species occurring in the riverine sections at the upper ends of the reservoirs. Littoral habitat in the reservoirs supports varying amounts of vegetation with moderate amounts of standing timber (Kinney et al. 2001).

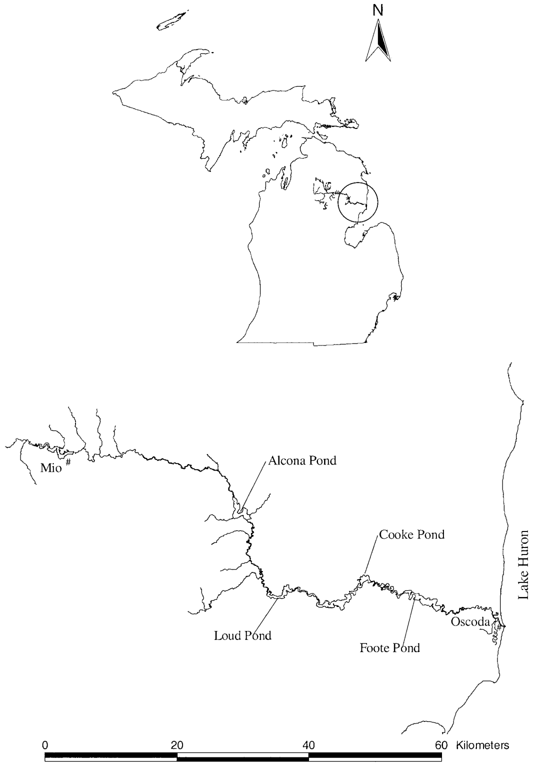

FIGURE 1.—Maps showing the locations of the Au Sable River, Michigan (top), and the four study reservoirs (bottom).

TABLE 1.—Physical and limnological characteristics of the Au Sable River study reservoirs based on data from Consumer's Power Company, the Federal Energy Regulatory Commission, the U.S. Forest Service, and this study. Reservoirs are ordered from upstream to downstream. The values for chlorophyll *a* and total phosphorus are mean summer values from samples taken in June through August of 2000 and 2001.

Reservoir	Surface area (ha)	Mean (maximum) depth (m)	Retention time (d)	Secchi depth (m)
Alcona	407	3.8 (12.2)	5.2	1.7
Loud	301	2.9 (7.9)	2.5	1.9
Cooke	658	5.0 (11.6)	9.4	3.4
Foote	689	5.8 (10.7)	11.4	3.9

Experimental Approach

The Northeast Michigan Sportsman's Club constructed and placed habitat enhancement structures (half-logs and AquaCribs; described below) in Loud, Cooke, and Foote ponds in the fall of 1999. In 2001, we placed structures in Alcona Pond as well as additional structures in Loud Pond. We conducted within-reservoir comparisons between areas with and without structures after structure placement in these four reservoirs. In addition, in Alcona Pond we conducted within-reservoir comparisons before and after the placement of structures (Table 2). In all four reservoirs, sites were chosen for treatment (structure) and reference (no structure) pairs to ensure that within pairs the treatment and reference areas were as morphometrically similar to each other as possible and that the paired sites represented a variety of habitat conditions (substrate type, coarse woody material cover, and macrophyte cover) throughout each reservoir. Reference areas were located a minimum of 100 m from the treatment areas. Whenever possible, we paired one treatment area with one reference area. When this was not possible, one reference area was shared between two treatment areas (altogether, five reference areas were paired with 10 treatment areas). Shared reference areas were placed a minimum of 100 m from the respective treatment areas in locations with similar natural habitat features (substrate type, coarse woody material cover, and macrophyte cover). The minimum distance between two consecutive treatment−reference pairs within reservoirs was 100 m, but the distance was typically at least 300 m.

The Northeast Michigan Sportsman's Club constructed the half-logs (a nesting and cover device) by bolting a masonry block to each end of one side of a flat hardwood slab (approximately 2.4 m in length, 25 cm in width, and 5 cm thick), leaving 5–10 cm of the slab overhanging at each end, similar to the half-log described by Hoff (1991). We arranged the half-logs so that they were perpendicular to the shoreline and 5 m apart at the 1-m depth contour in groups ranging from 4 to 97. AquaCribs, a box-shaped shelter device (122 × 152 × 122 cm) constructed of corrugated plastic, were placed in clusters varying in number from 3 to 10 suspended 1 m above the bottom over a depth interval of 2.7–5.5 m. The numbers of half-log and AquaCrib sites varied among reservoirs (Table 2).

Natural Habitat

To evaluate the effectiveness of half-log structures across different substrate types and levels of coarse woody material and macrophyte cover, we characterized the natural habitat at each treatment and reference pair using methods similar to those of Hunt et al. (2002). A diver wearing a snorkel and mask made visual observations of natural habitat conditions across the entire length of a line transect over the middle depth contour of each area

TABLE 2.—Experimental design and number of sites per reservoir. The term ''before–after'' indicates a within-reservoir comparison before and after structure placement. The term ''after only'' indicates within-reservoir comparisons of areas with and without artificial structures.

Experiment feature	Reservoir			
	Alcona	Loud	Cooke	Foote
Design and analysis	Before–after and after only[a]	After only	After only	After only
Year of structure placement	2001	1999 and 2001[b]	1999	1999
No. of half-log sites	10	11	10	9
No. of AquaCrib sites	0	0	8	23

[a] Data from 2000 and 2001 were used for the former, only data from 2001 for the latter.

[b] Some structures were placed in fall 1999; additional structures were placed in early summer 2001.

(see description of transects in the next paragraph). The diver noted and recorded substrate composition (sand, clay, or gravel), the presence and diameter of coarse woody material stems, and the presence and length of macrophyte patches. We calculated the percent cover of coarse woody material and macrophytes by summing the diameter or length of the respective habitat types along the line transect and dividing by the total length of the transect. Sampling took place once per site during early June of 2001 (to coincide with the nesting season) and once in early August of 2000 and 2001 (when macrophyte growth was near or at completion).

Fish Concentration

We estimated the relative abundance of fish using visual observation and electrofishing at half-log sites and gill netting at AquaCrib sites. Visual observations were made while snorkeling along line transects (modified from Keast and Harker 1977; Moring and Nicholson 1994; Brown et al. 2000). Divers wearing snorkels and masks conducted visual observations on the half-logs 1 d per week in each reservoir during the first 2 weeks of each month (June–August). Six treatment and reference pairs within a reservoir were randomly selected for observation on each sampling date. Separate divers swam each treatment and reference area of a pair simultaneously. At half-log treatment areas containing less than 10 half-logs, the divers conducted three parallel line transects to estimate fish abundance over the entire area where the half-logs were placed. The first transect was parallel to the shore at the nearshore end of the half-logs (1-m depth contour), the second at the middle of the half-logs, and the third at the deep end. At sites containing 10 or more half-logs, a random subsample of five half-logs was chosen for observation. Nearshore transects were located on the 1-m depth contour and proceeded in a downstream direction parallel to the shore, beginning 5 m before the first half-log encountered and ending 5 m after the last one. Upon completion of the first transect, the swimmer reversed direction and completed the second transect and then the third in an effort to minimize disturbance over the study area. Divers marked transect starting and ending points on the shoreline with surveyor's tape and used a removable buoy system to ensure that all transect lengths and depths were equal between treatment and reference pairs. Divers established transect lengths for each area on the first sampling date that a site was chosen for observation. All fish observed at each transect were identified to species and counted. We calculated relative abundance (fish/km) by averaging the three line transect counts at each area and then dividing by the length of the transect.

Electrofishing at half-log sites was conducted once per month (June−August) in each reservoir. Field personnel made one transect in the downstream direction with a boat-mounted electrofisher (7 A pulsed DC; 120 Hz) on the 1-m depth contour at each of six treatment and reference pairs randomly chosen for sampling. Transects in reference areas were of the same length as transects in the corresponding treatment areas. Field personnel used the surveyor's tape attached to the shoreline from visual observation to mark the start and end of transects. All fish captured were identified to species and counted. We calculated relative abundance (fish/km) by dividing the total number of each species captured by the transect length.

Visual observation and electrofishing were not possible as sampling methods for AquaCribs due to the depths at which the AquaCribs were placed. As a result, we used catches by gill nets (15.24 m long and 1.83 m deep, with four-panel experimental mesh of 1.3-, 1.9-, 2.5-, and 3.8-cm mesh size) to estimate relative fish abundance. Twice per month (June–August), we conducted netting at each reservoir. The treatment and reference areas were sampled concurrently at similar depths with separate nets. In 2000, we set the nets at the depth contour past the last visible cribs (4.6–5.5 m) in midmorning and removed them in the late afternoon. A short set was used to minimize mortality; however, few fish were caught during this time period. Therefore, in 2001 we set the nets in late afternoon and removed them the next morning. Field personnel counted and recorded all of the fish species captured to provide estimates of relative abundance (catch/h).

Attraction of Nesting Fish

We used visual observation (modified from Hunt et al. 2002) to evaluate the use of half-logs by nesting smallmouth bass. Sampling took place two to three times per week during May and early June in Cooke and Foote ponds in 2001. Divers wearing snorkels and masks sampled each treatment and reference pair within the reservoir on each sampling occasion. The divers swam transects over the middle depth contour of half-log treatment areas and over the same depth contour in reference areas using the visual observation protocols described above. Each nest encountered within 2 m of the transect was assigned a unique number and marked by means of a piece of surveyor's tape attached to a large metal washer. All nests were checked each time the transect was sampled. The divers recorded nest number, substrate, and the presence or absence of fry (the metric of nest success).

Angler Catch Rates

We used standardized angling to evaluate the effectiveness of both half-logs and AquaCribs in concentrating fish for angler capture. Once per month per reservoir during June, July, and August 2000 and once per week per reservoir during the same months of 2001, two anglers fished six randomly selected treatment and reference pairs for 10 min each with randomly assigned artificial or live baits. The first location to be fished within each pair (treatment or reference) was assigned randomly; individual baits and lures were randomly assigned to each angler. Anglers counted and recorded all fish species captured to provide estimates of relative abundance (catch/h).

Statistical Analyses

To facilitate data analysis and interpretation, we included in our analysis the nine most abundant game fish species, namely, black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, largemouth bass *M. salmoides*, northern pike *Esox lucius*, pumpkinseed *L. gibbosus*, rock bass *Amblopites rupestris*, smallmouth bass, walleye *Sander vitreus* (formerly *Stizostedion vitreum*), and yellow perch *Perca flavescens*. We first evaluated the aggregate response of these nine species (hereafter referred to as the ''total'' response). Next, we divided the nine species into three mutually exclusive groups: smallmouth bass, other piscivores (largemouth bass, northern pike, and walleyes), and planktivores (black crappies, bluegills, pumpkinseeds, rock bass, and yellow perch). All data were analyzed with SAS (SAS Institute, Inc. 1999). When appropriate, we transformed the data to meet the necessary distributional assumptions. The rejection criterion was set at $\alpha = 0.05$ for all analyses.

Treatment–reference area comparisons.—We used data collected from Cooke and Foote ponds in 2000 and 2001 and data collected from Alcona and Loud ponds in 2001 for within-reservoir comparisons between treatment and reference areas (Table 2). In order to extrapolate the results beyond the four reservoir systems studied, we used mixed-effect analysis of variance (ANOVA; PROC MIXED, SAS Institute, Inc. 1999). We determined whether the mean difference in relative abundance for each fish group, derived from both visual observation and electrofishing, varied predictably as a function of substrate type, coarse woody material cover, and macrophyte cover. We conducted a similar analysis to determine whether the mean difference in smallmouth bass nest density and nest success in treatment versus reference areas varied predictably as a function of substrate type, coarse woody material cover, and macrophyte cover. For each fish group, we again used mixed-effect ANOVA to determine whether the mean difference in relative abundance derived from angling and gill netting varied predictably as a function of treatment. For all mixed-effect models, we treated treatment and substrate as fixed effects and reservoir and site (nested within reservoir) as random effects. The percent cover of coarse woody material (CWM) and macrophytes were treated as covariates.

Pre- versus posttreatment comparisons.—We used data collected from Alcona Pond in 2000 and 2001 for within-reservoir comparisons before and after structure placement. We used mixed-effect ANOVA to determine whether the mean difference in relative abundance derived from visual observation and electrofishing (comparing treatment and reference areas) for each fish group varied according to year and treatment. Insufficient an-

TABLE 3.—*P*-values from a mixed-effect analysis of variance modeling the effects of treatment, macrophyte cover, coarse woody material (CWM) cover, and substrate on catch per effort by functional fish group (see text). Treatment refers to the presence or absence of half-log habitat enhancement structures; *N* = the total number of areas sampled; NS = not significant. No significant treatment effects were found for gill netting at AquaCribs (*N* = 67), angling at half-logs (*N* = 112), or angling at AquaCribs (*N* = 189).

Sampling method	Functional group	Treatment	Macrophyte cover (%)	CWM cover (%)	Substrate	Significant interactions
Visual observation (*N* = 369)	Total	NS	NS	NS	NS	None
	Planktivore	NS	NS	NS	NS	None
	Piscivore	NS	<0.0001	<0.016	NS	None
	Smallmouth bass	<0.022	NS	<0.003	NS	None
Electrofishing (*N* = 235)	Total	NS	NS	NS	NS	None
	Planktivore	NS	NS	NS	NS	None
	Piscivore	NS	NS	NS	NS	None
	Smallmouth bass	<0.020	NS	<0.045	NS	Treatment × macrophyte cover (<0.018)

gling data were collected to permit comparisons before and after structure placement. We treated treatment and year as fixed effects and site as a random effect.

Results

Fish Concentration

Half-logs within reservoirs.—Effects of half-logs on fish catch per effort (CPE) were detected primarily for smallmouth bass. The presence of half-logs had a significant positive effect on smallmouth bass abundance, as indicated by the mixed-effect models for both visual observation and electrofishing (Table 3; Figure 2). Although no other significant effects of half-logs on CPE were documented, in most cases (the one exception was piscivore CPE from the visual observation samples), point estimates of mean CPE were higher in

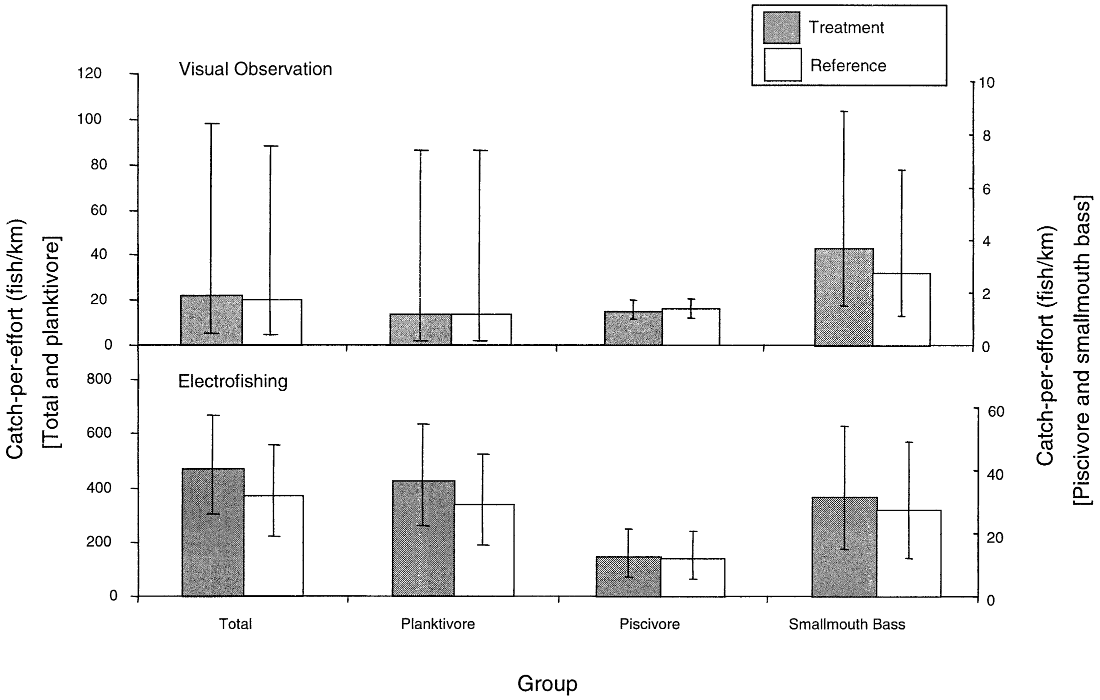

FIGURE 2.—Mean back-transformed catch per effort of the four functional fish groups defined for this study (see text) in the treatment and reference areas as determined by visual observation (top panel) and electrofishing (bottom panel). The thin vertical lines represent the 95% confidence intervals. Note that the *y*-axes differ depending on the functional group and sampling method.

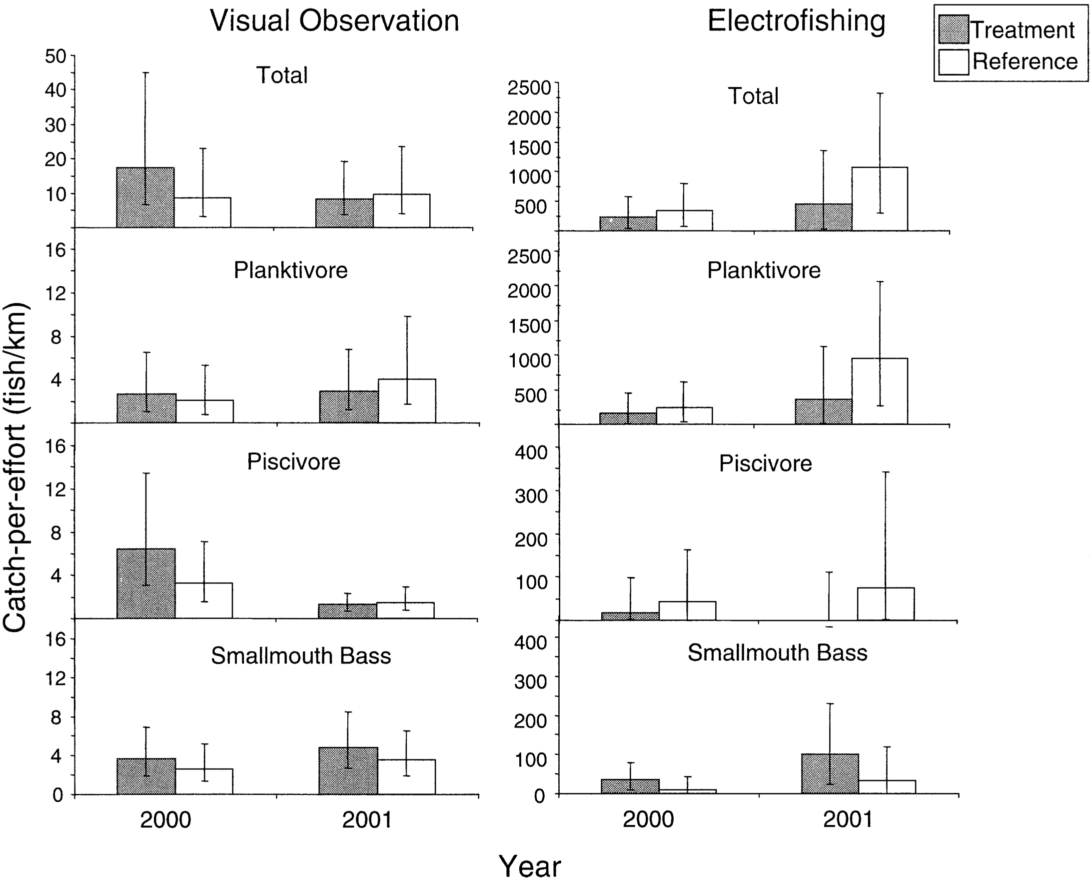

FIGURE 3.—Mean back-transformed catch per effort of the four functional fish groups defined for this study (see text) in the treatment and reference areas as determined by visual observation (left-hand panels) and electrofishing (right-hand panels) before (2000) and after (2001) structure placement in Alcona Pond. The thin vertical lines represent the 95% confidence intervals. Note that the *y*-axes differ depending on the functional group and sampling method.

treatment areas than in reference areas (Figure 2). The catch per effort of all fish groups was higher for electrofishing than visual observation, although the patterns of relative abundance among fish groups were similar between the two sampling methods (Figure 2).

Two fish groups, piscivores and smallmouth bass, showed significant variation with respect to CWM and macrophyte cover (Table 3), although the direction of response to habitat differed among habitat types and between fish groups. Piscivore CPE from visual observation decreased with increasing macrophyte cover but increased with increasing CWM cover. Similarly, smallmouth bass CPE, both from visual observation and electrofishing, increased with CWM cover. In addition, electrofishing data indicated the presence of a significant treatment × macrophyte cover interaction for smallmouth bass CPE. Smallmouth bass CPE at treatment areas containing half-logs decreased with increasing macrophyte cover, while the opposite trend was present at reference areas. Hence, smallmouth bass CPE at treatment areas most exceeded reference area CPE at sites with low macrophyte cover.

Half-logs pre- and posttreatment.—In Alcona Pond, no significant treatment × year interaction occurred for any of the four fish groups, indicating that half-log structures did not significantly concentrate fish after their placement (Figure 3). Year presented a significant source of variability, piscivore CPE being significantly higher in 2000 than in 2001 for visual observation ($F = 12.01$; df $= 1, 79$; $P < 0.001$) and total and planktivore

TABLE 4.—*P*-values from a mixed-effect analysis of variance modeling the effects of treatment, macrophyte cover, coarse woody material (CWM) cover, and substrate on smallmouth bass nest density and nest success. A total of 126 individual nests were monitored throughout the entire spawning season in 2001. Treatment refers to the presence or absence of half-log habitat enhancement structures; NS = not significant.

Metric	Treatment	Macrophyte cover (%)	CWM cover (%)	Substrate	Significant interactions
Nest density	<0.002	<0.003	NS	<0.046	Treatment × macrophyte cover (<0.010)
Nest success	<0.025	NS	NS	<0.013	Treatment × macrophyte cover (<0.017)

CPE being significantly higher in 2001 for electrofishing (total: $F = 9.07$; df = 1, 44; $P < 0.004$; planktivores: $F = 10.10$; df = 1, 44; $P < 0.003$). Treatment was significant for smallmouth bass sampled by electrofishing across both years ($F = 4.22$; df = 1, 44; $P < 0.046$), with higher CPE in treatment areas than in reference areas (Figure 3) both before and after structure placement.

AquaCribs within reservoirs.—The presence of AquaCribs had no significant effect on the concentration of any of the four fish groups. Mixed-effect models of mean gill netting CPE by fish group at AquaCribs indicated no significant treatment effect of AquaCrib structures.

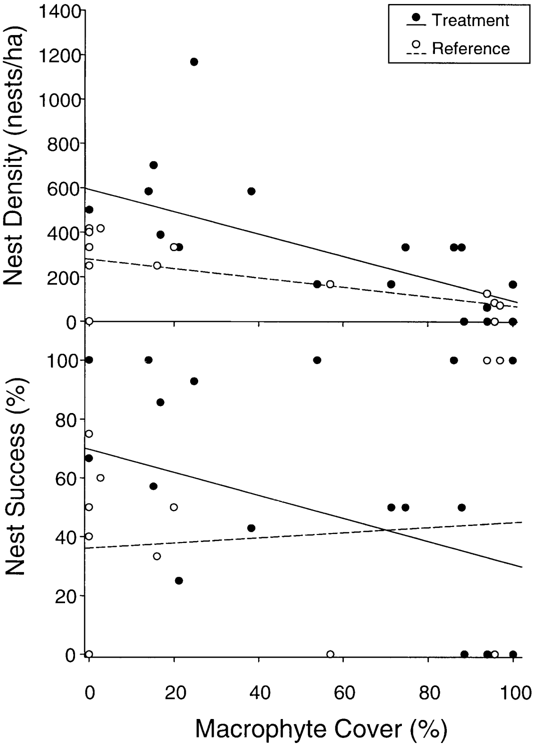

FIGURE 4.—Relationships between macrophyte cover and smallmouth bass nest density (top panel) and nest success (bottom panel) in the treatment and reference areas as determined by data collected in 2001 in Cooke and Foote ponds. The solid lines are best-fit lines for treatment areas; reference areas are represented by dashed lines.

Attraction of Nesting Fish

Smallmouth bass nest density was significantly higher in treatment areas with half-logs (mean = 357.4 nests/ha, 95% confidence interval [CI] = 257.3–457.5) than in reference areas (mean = 221.5 nests/ha, 95% CI = 112.2–330.8; Table 4). In addition to being more numerous, the nests in the treatment areas were also more likely to produce fry, with back-transformed mean values for nest success in treatment and reference areas of 47.2% (back-transformed 95% CI = 21.1–75.3%) and 36.6% (9.6–69.5%), respectively (Table 4).

Substrate and macrophyte cover were important factors affecting nest density and success (Table 4). Both metrics of reproduction were highest in areas with gravel substrate. Nest density averaged 416.7 nests/ha (95% CI = 289.4–544.0) in habitat with gravel substrate, with progressively lower values at clay (mean = 259.2 nests/ha, 95% CI = 53.9–464.5) and sand (mean = 192.5 nests/ha, 95% CI = 74.7–310.3) substrates. Nest success differed even more markedly among substrates, ranging from 87.6% (back-transformed 95% CI = 57.1–100%) at gravel substrates to 19.9% (1.2–74.1%) and 17.9% (1.4–46.9%) for clay and sand sites, respectively. Generally, macrophyte cover negatively affected nest density and success, particularly in treatment areas. Mean nest density decreased with increasing percent macrophyte cover at both treatment and reference sites. In addition, a significant treatment × macrophyte cover interaction was present for mean smallmouth bass nest density and nest success. Mean nest density and nest success were higher at treatment areas than at reference areas at low macrophyte cover, but this pattern became less noticeable as macrophyte cover increased (Figure 4). In other words, the positive effects of treatment on nest density and nest success are realized at sites with low percent macrophyte cover.

Angler Catch Rates

The presence of half-logs or AquaCribs had no influence on angler catch rates for any of the four fish groups. Mixed-effect models of mean angling CPE data by fish group at half-logs and AquaCribs indicated no significant treatment effects for either structure type.

Discussion

In addition to determining the extent to which habitat enhancement structures concentrate fish and influence nesting smallmouth bass, we sought to examine the interactive effects of structures, substrate, coarse woody material, and macrophytes. Our findings demonstrate the pervasive role that habitat variables, especially substrate and macrophytes, can play in determining the use of structures. The differences in visual observation and electrofishing CPE among reservoirs and sites within reservoirs typically exceeded the differences between treatment and reference sites (Wills 2002). Further, when treatment effects occurred, most of the significant patterns resulted from the interactions between macrophytes and habitat enhancement structures rather than from the effects of structures alone.

While the earliest work conducted in lentic systems indicated that the effectiveness of habitat enhancement structures at concentrating fish is influenced by structure type and the species present (Hubbs and Eschmeyer 1937; Rodeheffer 1939, 1945), more recent research has found variability in the effectiveness of structures due to the inherent characteristics of the system under study. For example, basin morphometry and the amount of alternative habitat available in the form of old habitat enhancement structures and fallen trees negatively affected structure use by fish in research conducted by Mitzner (1981). Rogers and Bergersen (1999) demonstrated that habitat enhancement structures effectively concentrated adult largemouth bass in previously underutilized regions of two warmwater impoundments in the absence of lush macrophyte beds. Recognition of such relationships between natural habitat and structure effectiveness can improve the overall efficacy of future projects.

In our study, the effects of habitat enhancement structures varied among the fish species examined. While other studies have demonstrated the positive effects of structures on several species (Rodeheffer 1945; Wilbur 1978; Moring et al. 1989), we documented positive effects only for smallmouth bass. The relative abundance (from visual observations and electrofishing), nest density, and nest success of smallmouth bass were higher at half-log treatment areas, but angler catch rates were not affected by the presence of half-log structures.

Previous studies also have indicated that black bass (*Micropterus* spp.) demonstrate an affinity toward structures (Prince and Maughan 1979a, 1979b; DuFour 1989; Rogers and Bergersen 1999). In addition to congregating at structures throughout the summer, black bass display a preference for structures during the nesting season. Vogele and Rainwater (1975) found high numbers of spawning spotted bass *M. punctulatus* and largemouth bass around brush shelters in an Arkansas reservoir but noted that smallmouth bass showed no preference for the brush structures. Coble (1975) and Miller (1975) noted that smallmouth bass preferred overhead cover throughout all life stages, including nesting. Accordingly, Hoff (1991) documented dramatic increases in smallmouth bass nest density, nest success, and juvenile abundance after treatment with half-logs in northern Wisconsin lakes in which CWM was not abundant. Patrick (1996) found similar results for smallmouth bass nest density and nest success in a Tennessee reservoir. Hunt et al. (2002) determined that spawning largemouth bass were attracted to half-log structures, but the degree to which this occurred was dependent on the amount of complex physical habitat nearby. Our results are consistent with those of Hoff (1991), Patrick (1996), and Hunt et al. (2002). Half-log habitat enhancement structures significantly increased smallmouth bass nest density and nest success in comparison with areas without structures. However, natural habitat conditions were an important factor in determining nest density and nest success in areas with structures. As Hunt et al. (2002) discovered for largemouth bass, the characteristics of available physical habitat such as substrate and macrophyte cover played a key role in determining the abundance of smallmouth bass nests near half-logs.

Substrate as well as structure affects nesting smallmouth bass. Vogele and Rainwater (1975) noted that nesting smallmouth bass in an Arkansas reservoir appeared selective toward substrates of rocks and gravel. Wiegmann et al. (1992) found that male smallmouth bass in a northern Wisconsin lake that constructed nests over rocky substrate were more likely to attract a mate than those that constructed nests in sandy substrates. The authors also documented that the nest was rarely successful when the within-nest substrate was composed of sand, while the survival of young was greatest in nests with rocky substrates. In addition, survivorship was greater in pebble nests than in nests predominantly composed of vegetation. Our results agree with those of both Vogele and Rainwater (1975) and Wiegmann et al. (1992). Smallmouth bass nest density and nest success were higher in areas with gravel substrate than in areas with clay and sand substrate regardless of the presence of half-logs. However, when half-logs were present nest density and nest success increased across all substrate types, reinforcing the important effect of the habitat enhancement structures.

Habitat enhancement structures are often installed to improve angling opportunities, but if fish vulnerability to angling increases more than fish production overharvest could result. Accordingly, standardized angling has been a widely used method for evaluating the effectiveness of structures in attracting fish and increasing angler catch rates (Wilbur 1978; Paxton and Stevenson 1979; Wege and Anderson 1979; Rogers and Bergersen 1999). Surprisingly, we found no difference in angler catch rates between treatment and reference sites. Our findings are counter to those of several previous studies that have demonstrated that angler catch rates are higher in areas with habitat enhancement structures (Wilbur 1978; Paxton and Stevenson 1979; Wege and Anderson 1979; Rogers and Bergersen 1999). In particular, two studies (Paxton and Stevenson 1979; Rogers and Bergersen 1999) have documented that habitat enhancement structures increase angler catch rates of black bass. Because these studies used different structures than ours (tires and synthetic ‘‘bass bungalows’’), we cannot determine the extent to which our contrasting findings are due to the specific type of structures used, the available natural habitat, or the characteristics of the bass populations.

Ultimately, guidelines for the efficacy of structure placement will require comparison of structure types in addition to evaluation of habitat influences on structure effects. Hubbs and Eschmeyer (1937) were the first to realize that structure types vary in their effectiveness at concentrating fish. Brouha (1974) noted that centrarchid species displayed a preference for reefs constructed of trees over reefs constructed of tires. Similarly, Rogers and Bergersen (1999) noted that largemouth bass displayed varying preferences toward different types of synthetic structures. Although we did not directly compare the effectiveness of half-logs and AquaCribs, we feel that it is important to note that half-logs (the simpler of the two structures we studied) appeared to be more effective in systems in which both half-logs and AquaCribs were installed. Whereas half-logs provide simple structure, AquaCribs provide complex structure, which is abundant in our systems in the form of macrophytes. In systems lacking complex cover, AquaCribs may be a better choice for habitat enhancement projects. Half-logs are also considerably less expensive than AquaCribs, are composed of materials readily available for purchase at any hardware store or lumberyard, and are simple to assemble.

In summary, we suspect that the natural habitat conditions present in the reservoirs that we studied limited the effectiveness of the habitat enhancement structures in concentrating fish. Coarse woody material and macrophytes were fairly abundant, indicating that natural habitat was probably less limiting than in many other reservoir systems. Accordingly, for our study reservoirs as a whole, the amount of habitat enhancement structures added was relatively small. We believe that this contributed to the paucity of significant structure effects in our study. In other words, the number of structures added was insufficient to attract most fish and increase concentration.

Fisheries managers must carefully consider the system as a whole when undertaking any habitat enhancement effort. Managers should determine the need for such projects by considering the amount, types, and distribution of natural habitat available within a particular system, as habitat enhancement structures may or may not work depending on just what habitat is a limiting resource for a population. In addition to the local habitat features that influence the effects of habitat enhancement structures (as demonstrated in this study and Hoff 1991), broadscale habitat features also may be quite influential. For example, in the case of nesting smallmouth bass in an Ontario lake, Rejwan et al. (1997, 1999) demonstrated that habitat features at the 1-km scale (such as temperature and shoreline complexity) are more important in determining the occurrence of smallmouth bass nests than habitat features at the 100-m scale. Thus, habitat features at several spatial scales should be integrated to identify the waters and sites most likely to benefit from habitat enhancement structures.

Additionally, managers may also consider placement of structures with regards to the species present within the system and their life history and habitat needs to ensure greater chances of success.

For example, smallmouth bass, a species that has demonstrated an affinity for overhead cover (Coble 1975; Miller 1975) and has benefited from structures in the past (Hoff 1991; Patrick 1996), responded positively in our study. Through consideration of such species-specific habitat preferences, as well as available natural habitat and the cost-effectiveness of various structure types, fisheries managers can plan beneficial and economical habitat enhancement efforts.

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