

Effectiveness of Bowfin as a Predator on Bluegill in a Vegetated Lake

NEAL D. MUNDAHL,* CHRISTINA MELNYTSCHUK, DEENA K. SPIELMAN,
JASON P. HARKINS, KATE FUNK, AND ANDREW M. BILICKI

Department of Biology, Winona State University
Post Office Box 5838, Winona, Minnesota 55987-5838, USA

Abstract.—Adult bowfins *Amia calva* were reintroduced (initial density approximately 32 fish/ha) into Lake Winona, Minnesota, from 1984 to 1986 to evaluate their effectiveness in controlling overabundant, stunted bluegills *Lepomis macrochirus* and other sunfishes (centrarchids) in a system with extensive macrophyte beds. Bowfin catch rates (trap nets, gill nets and electrofishing) declined rapidly after reintroductions ended in 1986. Catch rates and growth rates of bluegill and black crappie *Pomoxis nigromaculatus* have not changed since bowfin reintroduction. In 1992, only adult bowfins (average age, 10 years; average weight, 2.4 kg) were captured in Lake Winona, and they were concentrated in or near dense macrophyte beds. The final population estimate for bowfin in the west basin was 114 fish (3.17 fish/ha). Captive bowfins exhibited no size selection when feeding on sunfish and consumed on average less than 5 sunfish/24 h. Bowfin consumption rates declined by 80% when the density of artificial vegetation exceeded 500 stems/m². Bowfins preferred both fathead minnows *Pimephales promelas* and virile crayfish *Oronectes virilis* over sunfish in prey choice trials. Lack of natural reproduction by bowfins in Lake Winona, their rapid decline in numbers after stocking, and their low rate of sunfish consumption may explain why bowfins apparently have been ineffective in controlling the lake's bluegill population.

Populations of stunted bluegills *Lepomis macrochirus* can decrease the value of recreational fisheries in North American lakes, ponds, and reservoirs by producing small fish that are unacceptable to most anglers. Historically, many different approaches have been tested to increase bluegill growth rates. Stocking of predatory fish, primarily game fish such as largemouth bass *Micropterus salmoides* and northern pike *Esox lucius*, has been one of the more commonly applied management techniques. However, fisheries managers frequently are frustrated by the inability of these predatory game fishes to adequately regulate centrarchid populations (e.g., Beyerle 1971, 1978; Flickinger and Clark 1978; Noble 1981). Problems are most apparent in systems with extensive beds of aquatic macrophytes because bluegills tend to spend the majority of their time within the vegetation (Fish and Savitz 1983), where the feeding success of piscivorous fishes may be greatly reduced (Savino and Stein 1982; Gotceitas and Colgan 1987).

The Minnesota Department of Natural Resources (MDNR) began a project in 1984 that used the bowfin *Amia calva* as a predator on stunted bluegills and other sunfishes in Lake Winona, a lake plagued by dense vegetation. The bowfin was selected for stocking because of its preference for shallow, heavily vegetated habitats (Gill 1906;

Burgess and Gilbert 1980; Trautman 1981) and its apparent appetite for young sunfish (Scott 1938; Lagler and Hubbs 1940; Lagler and Applegate 1942; Berry 1955; Dugas et al. 1976). Early investigators called for the destruction of bowfins because of their predation on and competition with favored game fishes (e.g., Scott 1938). However, Scarnecchia (1992) reviewed the potential role of the bowfin in fishery management and called for new research to examine the function of the bowfin in fisheries systems. We undertook a series of field and laboratory studies designed to assess the success of the Lake Winona bowfin stocking project. We examined bowfin abundance and feeding rates in comparison with fisheries data collected from Lake Winona by the MDNR before and after bowfin stocking to evaluate the effectiveness of bowfins in controlling the bluegill population.

Study Site

Lake Winona is a 129-ha lake, lying in the natural floodplain of the upper Mississippi River in Winona, Minnesota. The lake is a former river side channel that was cut off from the river when tributary streams deposited alluvial sediments upstream and downstream from the present lake (Fremling and Heins 1986). A causeway separates the lake into east (93 ha) and west (36 ha) basins. The lake has an average depth of 2.5 m and a shoreline development index of 2.12 (Fremling

* Corresponding author: nmundahl@vax2.winona.msus.edu

and Heins 1986). The lake has been dredged several times to remove eroded agricultural soils transported to the lake during flooding of a local stream. Severe winterkills of fish occurred in Lake Winona during 1965 and 1969 (Fremling and Heins 1986).

In 1973, the lake underwent an extensive reclamation project to (1) remove rough fish and prevent their reintroduction; (2) aerate the lake to prevent fish winterkill; and (3) reintroduce game fish to provide an urban recreational fishery for the young, elderly, and handicapped (Fremling and Heins 1986). The reclamation was very successful, but in the early 1980s, aquatic macrophytes (primarily curlyleaf pondweed *Potamogeton crispus* and coontail *Ceratophyllum demersum*) became established in the lake and spread quickly to fill most of the littoral zone (85% of the total lake area). Increased vegetation provided protective cover for bluegills and other centrarchids (black crappies *Pomoxis nigromaculatus*, pumpkinseeds *Lepomis gibbosus*, green sunfish *L. cyanellus*), which became overabundant and stunted despite the presence of predators such as largemouth bass, northern pike, channel catfish *Ictalurus punctatus*, wall-eye *Stizostedion vitreum*, muskellunge *Esox masquinongy*, and flathead catfish *Pylodictis olivaris*. Spot chemical control and mechanical harvest failed to substantially reduce macrophytes, so 4,200 adult bowfins (7,666 kg total wet weight; 32.6 fish/ha) were reintroduced into Lake Winona from April 1984 to February 1986. Bowfins are native to Lake Winona, but were eliminated when the lake was treated chemically in 1973 to remove rough fish. Bowfins stocked into the lake were collected from nearby backwaters of the Mississippi River.

Methods

Field studies.—Fisheries population assessments of Lake Winona were conducted on a nearly annual basis by the MDNR (MDNR, unpublished fisheries surveys 1981, 1983–1990, 1992, 1994). Assessments included spring and fall electrofishing (five shoreline sites, 20 min/site) and summer trap netting (11–15 overnight sets of 76-cm-diameter net; 91 × 183-cm frame, 1.9-cm-bar-measure mesh, 1.1 × 12.2-m leads) and gill netting (5–7 overnight sets of 76-m nylon net; five equal-sized panels with 1.9, 2.5, 3.2, 3.8, and 5.1-cm mesh). Bowfin abundance in the lake was monitored before, during, and after the reintroduction period by evaluating gill-net, trap-net, and spring electrofishing catch rates for bowfin. Gill-net and trap-

net catch rates and growth rates for bluegill and black crappie were examined over the period 1981–1993 to detect changes that coincided with the bowfin reintroduction. Catch rates for bluegill and black crappie before and after bowfin stocking were compared with Mann–Whitney tests (Zar 1984). Changes in bluegill and black crappie length at age over the study period were examined with simple regression.

During July and August 1992, bowfin abundance was estimated in Lake Winona's west basin by multiple mark and recapture sampling. Fish were captured on 12 dates with a Coffelt CPS boomshocker mounted on a 5.3-m johnboat. On each date, electrofishing was conducted in a counterclockwise direction around the lake basin. No bowfins were collected in open-water areas during initial sampling, so subsequent sampling was focused on shoreline habitats and weed beds. Each bowfin was given a unique mark by using a paper punch to mark either individual fins or combinations of fins with small holes near fin margins. Fish were weighed to the nearest 0.2 kg, and measured (total length, TL) to the nearest 0.5 cm. Scales were collected from each fish for age determination, and fish were released at the point of capture. After the first sampling date, all bowfins were examined thoroughly for the presence of marks. Marks were easily recognized throughout the sampling period. Marked fish were recorded as recaptures, and unmarked fish received unique marks throughout the sampling period. Bowfin population size (with 95% confidence limits) within the west basin was then determined with the Schumacher–Eschmeyer modification of the Schnabel method (Krebs 1989).

Laboratory studies.—We attempted to examine prey selection by Lake Winona bowfins by examining their stomach contents, collected by pulsed gastric lavage (Foster 1977), but were unable to recover any food items. We therefore conducted feeding experiments on captive adult bowfins to determine size selectivity, feeding rates, prey preferences, and effects of macrophyte density on predation success. Bowfins were collected from Mississippi River backwaters near Lake Winona and were acclimated individually in 650-L rectangular tanks filled with aerated well water (16–19°C, flow-through rate of 2.5 L/min). Fish were exposed to a photoperiod of 12 h light : 12 h dark for a minimum of 2 weeks before experiments began. Prey species included sunfishes (mostly bluegills, but also a few pumpkinseeds and green sunfish; mean TL = 8.7 cm, mean wet weight =

14.3 g), fathead minnows *Pimephales promelas* (mean TL = 6.7 cm, mean wet weight = 2.6 g), golden shiners *Notemigonus crysoleucas* (mean TL = 11.3 cm, mean wet weight = 12.4 g), and virile crayfish *Orconectes virilis* (mean carapace length = 2.4 cm, mean wet weight = 5.6 g). Prey were either collected from local habitats or purchased from a local bait dealer. During acclimation, bowfins were offered a variety of prey types. All feeding experiments were conducted with a single bowfin in its acclimation tank. Bowfins were starved for 48 h before each experiment.

One experiment examined whether bowfins exhibited a size preference for sunfish. In two separate trials, individual bowfins (four in 1991, five in 1995; 51–63 cm TL) were offered premeasured size mixtures of sunfish (19–30 fish per bowfin; combined size range of 3.8–16.2 cm TL) for a 48-h period in experimental tanks devoid of both substrate and cover. At the end of the feeding period, remaining prey were collected, counted, and measured to determine which individual prey had been consumed. A contingency table analysis (*G*-test, log-likelihood ratio; Zar 1984) was used to compare the sizes of available versus consumed prey for all data pooled within each trial. Pooling was necessary because of low consumption rates by most bowfins. Sunfish were grouped into 10-mm sizes classes for analysis.

A second experiment examined bowfin feeding rates on different prey species. Seven bowfins (54–70 cm TL) were offered groups of either 15 fathead minnows, 7–10 golden shiners, or 20 sunfish for 24-h to 48-h periods. Bowfins usually were observed for the first hour after prey were introduced, and the number of attacks and number of prey consumed were recorded. After 24 and 48 h, the total number of prey consumed was recorded. The numbers of fathead minnows, golden shiners, and sunfish consumed were compared with Kruskal-Wallis tests for both 1-h and 24-h time periods (Zar 1984).

A third experiment examined feeding preferences of bowfins. Three different combinations of prey (20 sunfish and 7 crayfish, 10 sunfish and 10 fathead minnows, 10 fathead minnows and 8 crayfish) were offered to each of five bowfins (58–70 cm TL). The numbers of prey consumed during each prey choice trial were recorded after 1, 24, and 48 h to determine bowfin consumption patterns for each prey type. Chi-square tests were used to assess possible prey preferences over each time period. Because of low numbers of prey consumed by bowfins, especially over 1- and 24-h time pe-

riods, data from all bowfins were pooled before analysis.

A fourth experiment examined the predation success of bowfins on sunfish in tanks containing varying densities (0, 92, or 530 stems/m²) of artificial macrophytes. These artificial weed beds were constructed by fastening 50-cm lengths of braided polypropylene rope (6-mm diameter) in a uniform pattern to a wire mesh framework cut and weighted to fit the bottom of the tanks. Ropes floated in an upright position, simulating natural macrophytes. The three stem densities chosen for experimentation simulated macrophyte densities found in Lake Winona during late summer (weed bed stem density range = 92–600 stems/m² based on 10 plots, 0.1-m² each). Adult bowfins (five fish, 58–70 cm TL) in artificial-macrophyte tanks were presented with 20 sunfish and allowed to feed for 48 h, after which artificial macrophytes were removed and remaining prey were collected and counted. Each bowfin was tested at each stem density, with the order of testing at each stem density randomly selected for each fish. Two-factor analysis of variance (ANOVA) and Tukey's multiple comparison (Zar 1984) were used to compare sunfish consumption among the three macrophyte densities. Consumption by each bowfin was examined as a covariate to account for individual differences in consumption rate that might preclude detection of differences in consumption rate by bowfins among macrophyte densities.

Results

Bowfin Abundance

Trap netting, gill netting, and electrofishing in Lake Winona by MDNR revealed peak populations of bowfin in 1985 and 1986 (Figure 1). Catch rates of bowfin with all three sampling gears declined rapidly within 2–3 years after reintroductions ended in 1986 and have continued to decline since 1988–1989, though at a much slower rate. By 1993, catch rates of bowfin in Lake Winona were lower than state median catch rates for the species.

During 1992, 48 bowfins were captured in west Lake Winona, marked, and returned to the lake. These fish ranged in weight from 1.2 to 4.4 kg (mean = 2.4 kg), in length from 51.5 to 77.0 cm (mean = 63.5 cm), and in age from 7 to 18 years (mean = 10 years). Based on these captures, the estimated population size for bowfin in west Lake Winona was 114 fish, a density of 3.17 fish/ha (95% confidence limits = 71 [1.97 fish/ha] to 293 [8.14 fish/ha] bowfins). None of 12 bowfins col-

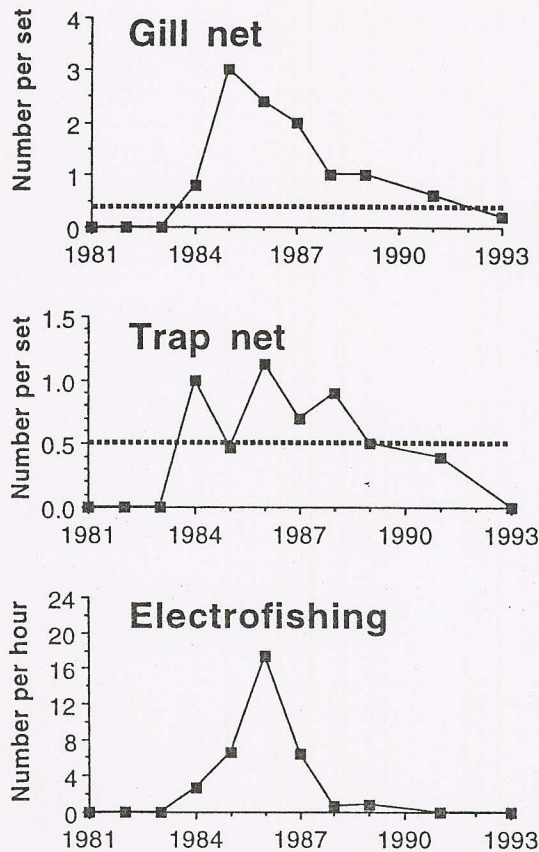


FIGURE 1.—Gill-net, trap-net, and electrofishing catch rates for bowfin in Lake Winona, 1981–1993. Dashed lines represent median catch rates for bowfin in Minnesota lakes (Minnesota Department of Natural Resources, unpublished annual fisheries surveys).

lected from east Lake Winona during the study period carried marks indicating prior capture in the west basin.

Sunfish Abundance and Growth Rates

Catch rates for bluegill and black crappie in Lake Winona from 1981 to 1993 in gill nets and

trap nets were not strongly correlated with each other (bluegill: Spearman rank correlation coefficient [r_s] = 0.55, P = 0.08; black crappie: r_s = 0.01, P = 0.97) but were above regional median catch rates for both species for both gear types (Table 1). Catch rates of bluegill and black crappie before (1981–1984) and after bowfin reintroduction (1985–1993) were not significantly different (Table 1).

Growth rates of bluegill and black crappie have changed little after bowfin reintroduction (Figure 2). Average lengths remained relatively consistent for all ages of bluegills and black crappies through the 11-year period, except that the average size of age-6 bluegills declined (F = 13.77, P = 0.01, r = 0.83).

Laboratory Feeding Experiments

In size selection feeding trials with sunfish as prey, the average size of fish consumed was 7.3 cm (SD = 2.4 cm, range = 4.2–12.0 cm). Although different sizes of prey were used during each trial, sizes of prey consumed by bowfins during both trials did not differ significantly from the sizes of prey offered (Figure 3; trial 1: G = 9.29, df = 11, P > 0.5; trial 2: G = 7.66, df = 10, P > 0.5). No sunfish over 13 cm TL was consumed by a bowfin during either trial.

When fathead minnows, golden shiners, or sunfish were offered separately as prey, bowfins consumed an average of 7.8 fathead minnows, 6.7 golden shiners, and 4.3 sunfish in 24 h (Table 2). The number of prey consumed did not differ between the three prey types over this period (Kruskal–Wallis H = 1.79, P = 0.41); however, bowfins consumed significantly fewer sunfish than fathead minnows or golden shiners during the first hour of feeding (Kruskal–Wallis H = 8.00, P = 0.02; Table 2). Twenty-nine percent of the fathead minnows, 63% of the golden shiners, and 19% of the sunfish were consumed during the first hour. Based on

TABLE 1.—Mean (SD) gill-net and trap-net capture rates of bluegill and black crappie in Lake Winona before (1981–1984) and after (1985–1993) reintroduction of bowfin. State median capture rates for Minnesota are included for comparison (Minnesota Department of Natural Resources, unpublished annual fisheries surveys).

Species and gear type	Capture rate (number of fish/set):			Mann–Whitney tests	
	State median	Before reintroduction	After reintroduction	U	P
Bluegill					
Gill net	1.6	16.3 (7.7)	28.9 (12.5)	24	0.36
Trap net	11.7	63.3 (26.3)	78.5 (38.8)	17	0.46
Black crappie					
Gill net	2.0	11.1 (5.9)	23.0 (17.9)	20	0.42
Trap net	2.7	19.1 (13.5)	20.0 (13.3)	15	0.49

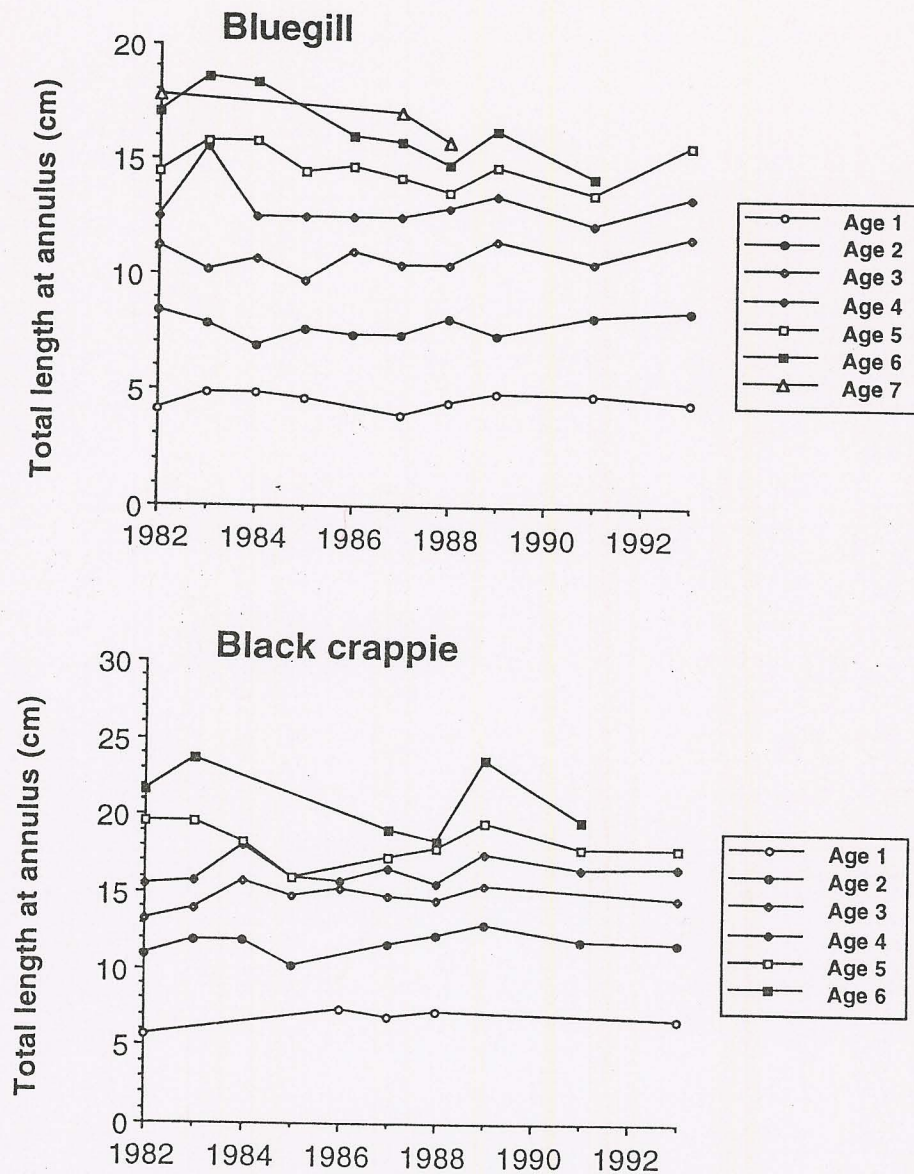


FIGURE 2.—Mean total length at annulus formation for bluegills (ages 1–7) and black crappies (ages 1–6) in Lake Winona, 1982–1993 (Minnesota Department of Natural Resources, unpublished annual fisheries surveys).

trials where bowfins were observed continuously for the first hour after prey introduction, bowfins captured an average of 39% of fathead minnows and 47% of golden shiners they attacked (Table 2). Bowfins were not observed during the first hour of sunfish trials, but based on the numbers of sunfish ingested (60) and wounded (31) after 1 h, capture rates were below 66%.

Prey preference trials indicated that sunfish were never the preferred prey when either fathead min-

nnows or crayfish were present (Table 3). Fathead minnows were strongly preferred over sunfish during 1-h, 24-h, and 48-h periods. Based on availability, crayfish were also chosen over sunfish during 1-h and 24-h periods. Fathead minnows were chosen more often than crayfish over 24-h and 48-h periods.

Sunfish consumption by bowfins differed among zero, low, and high densities of artificial macrophytes (two-factor ANOVA; $F = 5.57$; $df = 2, 8$; $P = 0.03$; Figure 4). Bowfins captured similar

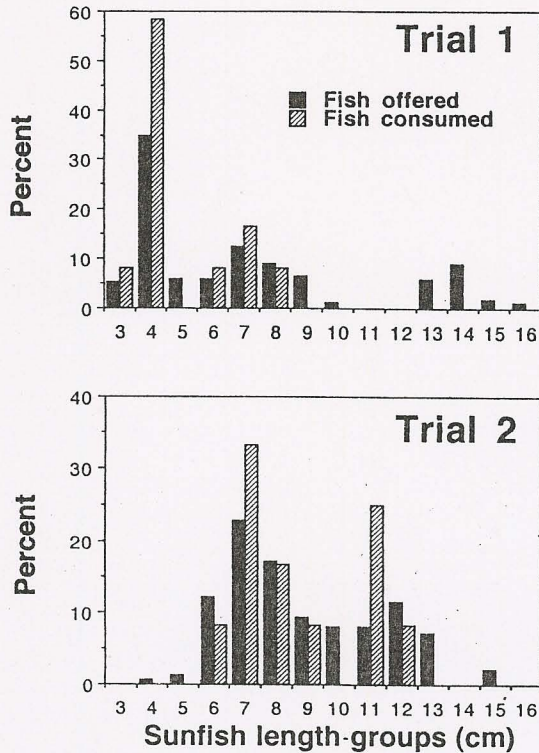


FIGURE 3.—Size distribution (total length, 1-cm length-groups) of sunfish offered to (trial 1: $N = 152$; trial 2: $N = 140$) and consumed by (trial 1: $N = 12$; trial 2: $N = 12$) captive bowfins during two separate trials.

numbers of sunfish at zero and low macrophyte densities, but significantly fewer fish at high macrophyte density. Consumption rates also differed significantly (two-factor ANOVA; $F = 4.25$; $df = 4, 8$; $P = 0.04$) among individual bowfins during these trials.

TABLE 2.—Mean (SD) attack and consumption rates per time period of seven bowfins feeding on 15 fathead minnows, 7–10 golden shiners, or 20 sunfish (*Lepomis* spp.) for 1, 24, and 48 h in the laboratory; ND = not determined.

Time period and measurement	Fathead minnows	Golden shiners	Sunfish
After 1 h			
Attacks	8.5 (2.9)	10.4 (3.2)	ND
Number consumed	2.3 (2.7)	4.2 (1.7)	0.8 (1.0)
Captures/attack	0.39 (0.13)	0.47 (0.20)	ND
After 24 h			
Number consumed	7.8 (5.4)	6.7 (1.8)	4.3 (4.4)
After 48 h			
Number consumed	ND	ND	6.6 (5.5)

TABLE 3.—Prey offered and consumed by five bowfins during 1-h, 24-h, and 48-h prey preference trials. Asterisks indicate preferred prey based on chi-square analyses ($P < 0.05$).

Trial and prey ^a	Number of prey offered	Number of prey consumed after		
		1 h	24 h	48 h
Trial 1				
Sunfish	50	0	5	6
Fathead minnows	50	22*	25*	31*
Trial 2				
Sunfish	100	3	18	35
Crayfish	35	7*	13*	15
Trial 3				
Fathead minnows	50	3	23*	28*
Crayfish	40	0	6	11

^a Sunfish were primarily bluegills but also some pumpkinseeds and green sunfish.

Discussion

Bowfins were reintroduced into Lake Winona to control stunted populations of sunfish but failed to reduce sunfish numbers or improve sunfish growth rates. This unique management technique may have been ineffective because (1) bowfin numbers declined precipitously in the few years following stocking, (2) bowfin feeding rates on sunfish were low, (3) sunfish were not a prey preferred by bowfin, and (4) bowfin feeding rates on sunfish were especially low in dense macrophyte beds.

Bowfin densities declined by 90% since they were last stocked in Lake Winona in 1986. This

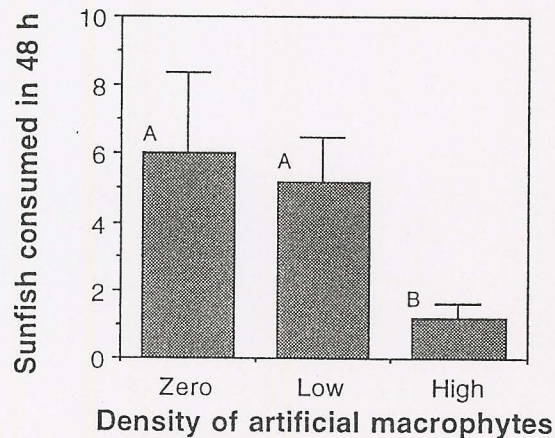


FIGURE 4.—Mean (+SE) 48-h consumption rates of five bowfins offered sunfish in laboratory tanks with zero, low (92 stems/m²), and high (530 stems/m²) densities of artificial macrophytes. Means not sharing a common letter are significantly different (analysis of variance and Tukey's multiple comparison, $P < 0.05$).

decline may have occurred because of reproductive failure, angling mortality, emigration, and natural mortality. Although nest construction has been observed (C. R. Fremling, Winona State University emeritus, personal communication), bowfins have not successfully reproduced or recruited in Lake Winona. Anglers also regularly catch and destroy bowfins (N. D. Mundahl, personal observation), despite an intensive public information campaign that explained the goals of the bowfin stocking program and encouraged anglers to release any bowfins caught (Fremling and Heins 1986). Bowfins also probably migrated out of the lake via two county ditches that connect to the lake because groups of bowfins were observed at these sites during April and May (Mundahl, personal observation). Finally, natural mortality of adult bowfins (observed regularly by Mundahl after spring ice-out) also contributed significantly to the decline in bowfin numbers observed in Lake Winona.

Laboratory feeding experiments suggest that bowfins may not be the voracious feeders they are believed to be (Breder 1928). Most bowfins in the laboratory consumed fewer than 5 sunfish/24 h, even after being starved for 48 h. These consumption rates may be higher than those of fish in the field because the confinement of sunfish permits predators to trap them in tank corners (Gillen et al. 1981). Only 2 of 13 bowfins examined from Lake Winona contained evidence suggesting consumption of more than one sunfish in the feeding period before sampling occurred (Mundahl, unpublished data). Stomachs of more than 200 bowfins collected in Michigan contained an average of only one fish and one crayfish per bowfin (Lagler and Hubbs 1940; Lagler and Applegate 1942). These rates of fish consumption are similar to those reported for esocids feeding on bluegills (Tomcko et al. 1984) but are considerably lower than those displayed by largemouth bass preying on bluegills in both field and laboratory experiments (Hayse and Wissing 1996).

Sunfish are seldom stunted in lakes with "good" populations of bowfin (Fremling and Heins 1986), so bowfins have been advocated as effective predators in controlling populations of stunted sunfish (Hubbs and Eschmeyer 1938; Roszman 1940; Scarnecchia 1992). Bowfins prey heavily on juvenile sunfish and crayfish in feeding studies (Gill 1906; Scott 1938; Lagler and Hubbs 1940; Lagler and Applegate 1942; Berry 1955; Dugas et al. 1976). Our findings also indicate that bowfins feed on sunfish, but that they generally prefer other

prey. Sunfish made up only 7–25% of the diets of bowfins in Michigan (19–51% of the fish numbers consumed; Lagler and Hubbs 1940; Lagler and Applegate 1942) and were consumed less frequently by bowfins in Missouri than either gizzard shad *Dorosoma cepedianum*, golden shiners, or bullheads *Ameiurus* spp. (Holland 1964). This apparent preference of bowfins for prey other than sunfish is probably caused by the lower vulnerability of sunfish to predation (Mauck and Coble 1971), which is the product of superior maneuverability, schooling behavior, body shape, and habitat use (e.g., Alexander 1967; Hall and Werner 1977; Gillen et al. 1981; Hambright 1991). Capture efficiencies of esocids (Wahl and Stein 1988) and largemouth bass (Gotceitas and Colgan 1987; A. Bilicki, Winona State University, unpublished data) are three to four times higher when feeding on fathead minnows (60–80%) than when feeding on bluegills (<20%). Although bowfins exhibited relatively low capture efficiencies (39–47%) on fathead minnows and golden shiners, they probably have even lower efficiencies when feeding on bluegills. In Lake Winona, alternate prey are relatively rare, which forced bowfins to feed with low efficiency on bluegills and other sunfishes.

The bowfin was selected for stocking in Lake Winona because of its purported ability to function in weed-filled waters (Gill 1906; Burgess and Gilbert 1980; Trautman 1981). Other piscivores have difficulty capturing prey within beds of vegetation (Savino and Stein 1982; Gotceitas and Colgan 1987; Hayse and Wissing 1996), which is where bluegills often spend much of the day (Hall and Werner 1977; Fish and Savitz 1983). Reductions in predator efficiencies within weed beds result from both changes in prey behavior and decreased predatory activity related to reduced visual contact with prey (Savino and Stein 1982). The results of our laboratory studies revealed that bowfins are no better than other piscivores at capturing sunfish in weed beds. Artificial macrophytes at high densities (530 stems/m²) caused an 80% reduction in sunfish consumption by bowfins, compared with feeding in weed-free tanks, which was similar to the 83% reduction in bluegill consumption reported for largemouth bass over a larger range (0–1,000 stems/m²) of macrophyte densities (Savino and Stein 1982). By contrast, tiger muskellunge (muskellunge × northern pike) displayed no reduction in bluegill consumption even in very high-density (2,000 stems/m²) weed beds (Tomcko et al. 1984).

Bowfins at the density stocked into Lake Winona (32 fish/ha), even with low consumption rates,

could consume large numbers of bluegills over a year. Bowfins, largemouth bass, and other piscivores were expected to consume over one million bluegills annually within 2 years after bowfin stocking, which would reduce bluegill numbers enough to increase growth rates and size structure (the initial population size was estimated at between five and six million fish; L. Gates, MDNR, personal communication). However, because bowfin density declined rapidly to below 10% of its original level only a few years after stocking, consumption of bluegills was never adequate to improve growth or size-structure of bluegills in Lake Winona.

Bowfin numbers have continued to decline in Lake Winona, and may be approaching their "natural" density of approximately 1.1 fish/ha (based on reclamation fish counts from Fremling and Heins 1986) that existed in the lake before reclamation in 1973. Additional stockings of bowfins are not planned. The current small population of bowfin probably will have little, if any, effect on bluegill numbers. Partial dredging is now being considered to deepen a portion of the lake and thereby reduce the area of weed beds. It is hoped that this would force more bluegills into open water where they are more vulnerable to predation (Gillen et al. 1981).

Management Implications

Factors such as the availability of alternative prey, presence of weed beds, and size of the bluegill population are important when bowfins are used as a predator for controlling stunted bluegills, but bowfin numbers must be sustained at a level that will significantly reduce bluegill densities. High bowfin density must be maintained, either through natural reproduction or continued stocking, to insure that adequate numbers are present to feed heavily on bluegills. If sustained stocking of bowfins had been possible for Lake Winona, positive effects on bluegills may have been observed. However, continued stocking of adult fish collected from natural habitats is a major undertaking and may be better geared to much smaller systems (e.g., <50 ha) than Lake Winona.

Before attempting to use bowfin again in a fisheries management role, we suggest that pond-based experiments be undertaken to more thoroughly examine how bowfin density, bluegill density, the presence of alternative prey, and vegetation influence the effectiveness of the bowfin as a predator on stunted bluegills. This information would be valuable in selecting systems where bow-

fin can make a positive contribution to the fishery. We also suggest that greater consideration be given to long-held negative attitudes toward the bowfin (Scarnecchia 1992). More intensive project publicity and legal protection of stocked bowfins may be necessary to counteract the negative feelings that many people have for this fish.

Acknowledgments

We thank Gary Grunwald (retired), Dan Dieterman, and Al Schmidt of MDNR-Fisheries, Lake City, Minnesota, for providing fisheries assessment data for Lake Winona. We also thank Doug Becher, Matt Johnston, Jason Rohweder, and Loryn Smith for assisting with field collections and laboratory set-up, and Randy Jackson for providing several obscure bowfin references. Calvin Fremling, Tim Schlagenhaft, Michael Delong, Steven Pothoven, Tim Cross, Michael Hansen, and two anonymous reviewers provided helpful comments on the manuscript and improved its clarity. A portion of this paper was based on a senior thesis submitted by Christina Melnytschuk in partial fulfillment of the requirements for Honors in Biology at Winona State University. This research was funded in part by a Winona State University Professional Improvement Grant.

References

- Alexander, R. M. 1967. Functional design in fishes. Hutchinson Publishing, London.
- Berry, F. H. 1955. Food of the mudfish (*Amia calva*) in Lake Newman, Florida, in relation to its management. Quarterly Journal of the Florida Academy of Sciences 18:69-75.
- Beyerle, G. B. 1971. A study of two northern pike-bluegill populations. Transactions of the American Fisheries Society 100:69-73.
- Beyerle, G. B. 1978. Survival, growth, and vulnerability to angling of northern pike and walleyes stocked as fingerlings in small lakes with bluegills or minnows. Pages 135-139 in R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland.
- Breder, C. M., Jr. 1928. On the appetite of *Amiatus calva* (Linnaeus). Copeia 1928:54-56.
- Burgess, G. H., and C. R. Gilbert. 1980. *Amia calva* Linnaeus, bowfin. Page 53 in D. S. Lee, and five coeditors. Atlas of North American freshwater fishes. North Carolina Biological Survey, Raleigh.
- Dugas, C. N., M. Kornikorf, and M. F. Trahan. 1976. Stomach contents of bowfin (*Amia calva*) and spotted gar (*Lepisosteus oculatus*) taken in Henderson Lake, Louisiana. Proceedings of the Louisiana Academy of Sciences 39:28-34.
- Fish, P. A., and J. Savitz. 1983. Variations in home ranges of largemouth bass, yellow perch, bluegills,

- and pumpkinseeds in an Illinois lake. *Transactions of the American Fisheries Society* 112:147-153.
- Flickinger, S. A., and J. H. Clark. 1978. Management evaluation of stocked northern pike in Colorado's small irrigation reservoirs. Pages 284-291 in R. L. Kendall, editor. *Selected coolwater fishes of North America*. American Fisheries Society, Special Publication 11, Bethesda, Maryland.
- Foster, J. R. 1977. Pulsed gastric lavage: an efficient method of removing the stomach contents of live fish. *Progressive Fish-Culturist* 39:166-169.
- Fremling, C. R., and G. A. Heins. 1986. *A Lake Winona compendium: information concerning the reclamation of an urban winter-kill lake at Winona, Minnesota*. Winona State University Press, Winona, Minnesota.
- Gill, T. 1906. Parental care among fresh-water fish. *Smithsonian Institution Annual Report* 1905:403-531.
- Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110:197-209.
- Gotceitas, V., and P. Colgan. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. *Transactions of the American Fisheries Society* 116:40-49.
- Hall, D. J., and E. E. Werner. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* 106:545-555.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500-508.
- Hayse, J. W., and T. E. Wissing. 1996. Effects of stem density of artificial vegetation on abundance and growth of age-0 bluegills and predation by largemouth bass. *Transactions of the American Fisheries Society* 125:422-433.
- Holland, H. T. 1964. Ecology of the bowfin (*Amia calva* Linnaeus) in southeastern Missouri. Master's thesis. University of Missouri, Columbia.
- Hubbs, C. L., and R. W. Eschmeyer. 1938. Improvement of lakes for fishing: a method of fish management. University of Michigan, Institute for Fisheries Research 2, Ann Arbor.
- Krebs, C. J. 1989. *Ecological methodology*. Harper and Row, New York.
- Lagler, K. F., and V. C. Applegate. 1942. Further studies of the food of the bowfin (*Amia calva*) in southern Michigan, with notes on the inadvisability of using trapped fish in food analyses. *Copeia* 1942:190-191.
- Lagler, K. F., and F. V. Hubbs. 1940. Food of the long-nosed gar (*Lepisosteus osseus oxyurus*) and the bowfin (*Amia calva*) in southern Michigan. *Copeia* 1940:239-241.
- Mauck, W. L., and D. W. Coble. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* 28:957-969.
- Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society* 110:738-750.
- Roszman, F. D. 1940. Dogfish data. *Ohio Conservation Bulletin*, (May):14.
- Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111:255-266.
- Scarnecchia, D. L. 1992. A reappraisal of gars and bowfins in fishery management. *Fisheries* 17(5):6-12.
- Scott, W. 1938. The food of *Amia* and *Lepisosteus*. *Investigations of Indiana Lakes and Streams* 1:112-115.
- Tomcko, C. M., R. A. Stein, and R. F. Carline. 1984. Predation by tiger muskellunge on bluegill: effects of predator experience, vegetation, and prey density. *Transactions of the American Fisheries Society* 113:588-594.
- Trautman, M. B. 1981. *The fishes of Ohio*. Ohio State University Press, Columbus.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117:142-151.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

Received July 11, 1997

Accepted November 13, 1997