American Fisheries Society Symposium 31:627–637, 2002

Demographic Changes in a Largemouth Bass Population following Closure of the Fishery

William A. Swenson[1]

Department of Biology and Earth Sciences and UW Extension,
University of Wisconsin–Superior,
Superior, Wisconsin, 54880-9948, USA

Abstract.—Changes in largemouth bass *Micropterus salmoides* abundance, age structure, survival, nesting activity, and reproductive success were measured in Little Rock Lake, Wisconsin, from 1983 to 1990. The creel fishery was closed in 1984 when the lake was divided into a reference (R-Basin) and a treatment basin (T-Basin), as part of an experimental acidification project. Largemouth bass abundance did not increase in response to the fishery closure. However, annual survival increased from 20 percent to 70 percent (R-basin). Average age increased from two, to five to seven years, and biomass increased at a rate of 0.66–0.68 $kg^{-1}ha^{-1}yr$ from 1985 to 1990. Sampling by angling catches increased from less than 100 to more than 500 g per hour. Nesting behavior and success were described by direct observation. Number of nests increased from a total of 41 (1984) to an average of 160 (1987–1988) and was positively correlated with spawner abundance. Nest predation declined significantly and nesting success (nests with swim-up fry) increased. August young of year (YOY) abundances also increased. Recruitment increased with estimated total length (TL) of young of year, but declined during years of high largemouth bass biomass. Cannibalism was common and appeared to influence recruitment. The results suggest that recent changes in Wisconsin fishing regulations will improve largemouth bass demographics and the quality of fishing.

Introduction

Little Rock Lake, Vilas County, Wisconsin, is an 18 ha low alkalinity (25 u eq/L) lake near the northern edge of the distribution range for largemouth bass *Micropterus salmoides*. The lake was closed to sport fishing from 1984 through 1990. Prior to the closure, largemouth bass were exploited under Wisconsin regulations from May through October, with a six fish daily bag and no size limit. In this paper, I describe changes in largemouth bass abundance, age structure, and survival in response to the fishery closure. Changes in nesting activity, nesting success, summer young of year (YOY) abundance, and relative recruitment at age 1 are also estimated. Catch rates and handling mortality are described from catch-and-release sampling.

Largemouth bass have been shown to be highly susceptible to fishing mortality. Bennett et al. (1991) suggested restrictive regulations are needed to maintain large fish in slow growing northern populations. Several studies indicate abundance, size structure, and fishing success improve when fishing mortality is reduced by lowering bag limits or by implementing minimum length, slot-length limits, or catch-and-release regulations (Rasmussen and Michaelson 1972; Barnhart 1989; Beamesderfer and North 1995). However, long-term studies involving closure of creel fisheries are relatively rare. Closure of the sport fishery on Round Lake, Wisconsin, from 1986 to 1989, resulted in increased abundance, age structure, mean total length (TL), and standing crop of largemouth bass (Otis et al. 1998). Catch rates increased dramatically when the fishery was re-opened to catch-and-release angling.

Larger male size has been linked to increased mating success and parental care (Philipp et al. 1997). Miranda and Muncy (1987) suggest that recruitment increases with size of spawners. Although not well documented, nest predation may be influenced by the size of nesting males and has been considered a limiting factor to largemouth bass reproductive success (Heidinger 1975). The Little Rock Lake fish species complex is dominated by a large yellow perch *Perca flavescens* population. Rock bass *Ambloplites rupestris* are abundant, and black crappie *Pomoxis nigromaculatus* are also present (Eaton et al. 1992). During this study, nesting activity was observed from 1984 to 1990, to determine if interspecific nest predation influenced

[1]Corresponding Author: wswenson@staff.uwsuper.edu, tel (715) 394–8410, fax (715) 394–8418

reproductive success and the relationship between nest predation and bass size.

Post et al. (1998) found predation by juvenile and adult largemouth bass on young of year influenced recruitment in Paul Lake, Wisconsin. Recruitment was reduced when predator density was high. Paul Lake is a small (1.7 ha) lake in which 95 percent of the fish biomass is largemouth bass. The Little Rock Lake study provided an opportunity to describe the relationship between juvenile and adult density and recruitment in a larger, more complex system.

The Little Rock Lake research program was designed as a whole ecosystem study of lake acidification. The lake was selected because its morphology allowed it to be divided into two basins. The lake was divided with a plastic curtain following a pretreatment study (September 1983–July 1984). The south basin (8.1 ha) was maintained at ambient pH 6.1, as a reference (R-Basin). The north basin (9.8 ha) served as a treatment (T-Basin) and was experimentally acidified to ph 5.6 (1985–1987), pH 5.1 (1987–1989), and pH 4.7 (1989–1991). The whole ecosystem approach is described by Watras and Frost (1989). Brazonik et al. (1993) describes the acid manipulations and ecosystem responses. Responses of all fish populations to the pH treatments are described by Eaton et al. (1992). The research team decided to close the fishery to protect field equipment and to control the number of variables influencing reproductive activity and success of fish populations. We hypothesized that the closure would result in increased abundance of spawners, more nests, greater nesting success, and increased largemouth bass YOY abundance.

The analysis of pH effects demonstrated that most largemouth bass demographics were not influenced by the pH treatments until late in the study (Eaton et al. 1992). Growth and survival of age-1 and older (≥ age-1) largemouth did not change. Nesting success and recruitment were not influenced in the T-basin until 1987. Therefore, during much of the study, observations from the two basins could be compared or pooled to describe the influence of the fishery closure on population demographics.

Methods

Largemouth Bass Demographics

Population abundance and age structure were described from samples collected by frame-nets, electrofishing and angling. Spring sampling was conducted during 1984–1990 from late April to the onset of spawning. Fall samples were collected from mid-August through mid-September or early October, 1983–1990. During some years, spring sampling was continued following spawning (late June through early July).

Annual angling sampling effort averaged 130 h per basin. Angling was used during all sampling periods and accounted for 71 percent of the age-1 and older largemouth captured. Members of the study team and guest anglers used boats equipped with tanks and were instructed to fish the whole shoreline of their assigned basin. A wide variety of artificial and live baits were used throughout the study.

Five sizes of frame-nets were used during the study. Nets were set throughout both basins during the spring and fall sampling periods. An average of 25, 24 hour sets were made in each basin per year and accounted for 21 percent of the largemouth bass captures. Small frame-nets (61 cm square frames with 0.6 cm mesh) were used to capture smaller size classes. Nets with 1.2 m square frames and 1 cm mesh were the most commonly used larger nets. Effectiveness of electrofishing was limited by the low conductivity of Little Rock Lake and accounted for six percent of the total captures. A 600 V-DC boom shocker was used one or two nights per year, primarily during the spring, prior to spawning when largemouth bass were near shore. Seines, dip nets, recovery of dead fish by snorkelers, and experimental gill nets accounted for less than two percent of the captures.

Captured fish were anesthetized (MS_{222}) and tagged (Floy FD67D t-bar anchor). Period-specific fin-scar marks were also applied (Welch and Mills 1981). Scale samples were collected, and TL (mm), wet weight (g), existing tag numbers, and batch marks were recorded. Starting in 1985, diet information was collected by stomach evacuation (Swenson and Smith 1973). After handling, fish were placed in recovery cages (0.6 × 0.6 × 1.9 m) for a minimum of two hours, prior to release. Handling and hooking mortality were estimated from mortalities that occurred in the cages and from dead fish recovered by surveying shorelines. The surveys were conducted along the whole shoreline of each basin by boat or snorkeling at the end of each sampling period.

Acetate impressions of scales were aged by two independent readers, and, for recaptured tagged fish, age was validated against previously assigned ages. For first captures, a third observer resolved differences between the first two readings.

Age structure of the population was expressed as the proportion of age-classes in yearly samples. Annual survival was estimated from catch curves (Ricker 1975) for the periods prior to and following closure of the fishery. Abundance was estimated by Chapman single census during 1984 and Jolly–Seber multiple recapture methods from 1985 to 1990 (Ricker 1975). The number and total weight captured per h of angling served as an index of relative abundance and of the potential change in the quality of fishing under catch-and-release management.

The number of spring spawners was estimated from fall population estimates of the number of age-3 and older largemouth. We assumed that age-3 and older largemouth bass spawn, based upon our observations of fish defending nests, and the results from a study which showed smallmouth bass captured off the nest in northern Wisconsin were age-3 and older (Raffetto et al. 1990). Average weight of spawning largemouth bass was estimated as a weighted average for the estimated number of age-3 and older largemouth bass in each basin.

Sampling during fall 1984 and spring 1985 indicated that largemouth bass had been unequally segregated during installation of the curtain. To ensure an adequate number of spawners and young in both basins, 671 young of year and 34 age-1 and older bass were transferred from the T-basin to the R-basin during 1985.

Reproduction-Early Life History

Largemouth bass nesting was described through snorkeling surveys conducted along the total shoreline of both basins to depths of approximately 2.5 m. Surveys were generally conducted twice per week on each basin throughout the spawning period, except during 1989–1990 when the observation schedule in the T-basin was reduced (approximately one survey per week). Snorkelers placed numbered marker rocks 2.5–3.0 m from each nest. While positioned near the markers, they recorded nest locations, substrate type, water depth, the number of juvenile and adult largemouth present, the presence of other species, and their interactions with guarding males or unguarded nest sites. After completing the general observations, observers swam near enough to describe the presence and general condition of embryos or fry. Embryos were described as translucent (live) or opaque (dead). All observations were recorded on acetate data sheets.

Predation on largemouth bass nests by yellow perch was identified by directly observing the behavior or from the presence of uprooted *Myriophyllum tenellum*. The macrophyte represented the substrate of most nests, and snorkelers observed that it was uprooted when yellow perch preyed on embryos in the nests. Nests which produced fry were identified as successful and were revisited until the broods dispersed. Nest formation was witnessed directly on some occasions. However, for most nests, the date of nest formation and abandonment were estimated from earlier observations at the location or from temperature and development rates relationships described by Allen and Romero (1975).

During August, young of year largemouth bass captured by minnow traps, seine, or small frame-nets were measured and marked with a small caudal clip. Snorkeling surveys of the complete shoreline of each basin were conducted to count marked and unmarked fish. The surveys were conducted by experienced observers who were instructed to count all YOY, but record only those for which they could clearly see the full outline of the caudal fin as marked or unmarked. The clips were visible at a range of 1.0–1.5 m, and observers generally reported 80 percent of the individuals encountered as marked or unmarked. Abundance was estimated using Chapman's single census method (Ricker 1975). During 1983, when no young of year were marked, and 1984 and 1987, when sample size was small, abundance was estimated from shoreline counts made by snorkelers (number per meter of shoreline). The counts for those years were multiplied by the proportion of the total population observed during years when abundance was estimated by mark–recapture. Relative overwinter survival and recruitment were interpreted through comparisons of August YOY abundances with catches of individual age-1 (excluding recaptures) per 100 captures of age-1 and older bass the following year. The recruitment index (RI) values were similar to the actual age-1 captures reported by Eaton et al. (1992) but corrected for differences in sampling effort, which occurred primarily during 1983–1984.

After the broods dispersed, growth was estimated from captures made by seine, minnow trap and by snorkelers using a calibrated mask-bar (Swenson et al. 1988). Instantaneous growth rates were described by regression analysis. Size differences between basins within a growing season were compared by analysis of covariance (ANCOVA). Mean TL, on 30 August, was estimated from the regression equations. Relationships among 30 August TL, YOY abundance, and relative recruitment were described by regression analysis.

Diet Analysis

Cannibalism and predation on yellow perch was described from stomach contents of 394 age-1 and older largemouth bass captured summer and fall during 1985–1990. Rates of cannibalism and predation on yellow perch for largemouth less than 300 mm TL were compared with those for larger fish (*t*-test). Relationships between the occurrence of young of year in stomachs and August YOY densities were described by regression analysis.

Results

Population Response to the Fishery Closure

Age was estimated from scales for a total of 886 largemouth bass. During the last three years, more than 85 percent were recaptured individuals. A total of 2,030 scale samples were analyzed to describe age structures. Age structure during 1983 and 1984 reflected the influence of the creel fishery and indicated that 95 percent of the population was comprised of ages 1 and 2 fish (Figure 1). Catch-curve analysis indicated that age-1 and older bass were captured in proportion to their abundance. Estimated annual survival of age-1 and older largemouth captured during 1983 and 1984, was 20 percent (Instantaneous Mortality $Z = 1.61$, $r^2 = 0.98$, $P < 0.01$). For the period following closure of the fishery (spring 1985–1990), survival was estimated from catches of strong 1982 and 1983 year-classes (ages 1–6), corrected for variation in annual sampling effort. Estimated annual survival for the R and T-basins were 70 percent ($Z = 0.35$, $r^2 = 0.56$, $P < 0.01$) and 90 percent ($Z = 0.11$, $r^2 = 0.42$, $P < 0.05$), respectively. Increased survival following the closure was reflected in increased abundance of older age classes. During 1987–1988 more than 60 percent of the largemouth bass in both basins were ages four and five (Figure 1).

Numerical abundance of largemouth bass was stable initially, then declined as the study progressed (Table 1). However, mean TL and weight increased from 193 mm and 111 g in 1984 to approximately 346 mm and 600 g mm by 1990 (Table 1). The larger size structure was reflected in increased biomass (Table 1). Unequal division of the population when the lake was divided also resulted in higher biomass in the T-basin throughout the study (Table 1). Biomass increased significantly at essentially the same rate (0.68 and 0.66 kg/ha) in the R and T-basins from 1985 to 1990 ($r^2 = 0.81$; $P < 0.01$).

Quality of fishing expressed as number and weight captured per hour reflected the changes in density and biomass (Table 1). Number captured per hour did not change. However, biomass catch per hour increased significantly at a rate of 46 g h^{-1} kg^{-1} ($r^2 = 0.83$; $P < 0.01$). Biomass catch per hour was approximately three times higher in 1990 than 1985. Annual handling mortality was three percent; one percent was attributed to angling, based upon field notations of deeply hooked fish.

Average annual tag loss was 1.7 percent. Fish identified as tag losses were not included in estimating recapture rates. Therefore, estimated recapture frequencies are lower than the actual rates. Estimated frequency of recapture ranged from 1 to

Table 1. Largemouth bass abundance, size, density and catch rates for Little Rock Lake (LRL) and for the reference (R) and treatment (T) basins.

		—Abundance—		Total length	Weight	— Density/— hectare		— Angling — CPE	
Year	Basin	No.[a]	(kg)	(mm)	(g)	No.	(kg)	No./h	(g/h)
1984	LRL	775	86	193	111	43	4.8	–	–
1985	R	218	35	218	160	22	4.3	0.6	101
	T	459	87	233	189	47	8.9	1.3	248
1986	R	212	32	220	151	26	4.0	0.4	66
	T	395	79	247	200	40	8.1	1.3	252
1987	R	158	49	269	307	20	6.0	0.5	150
	T	273	105	296	385	28	10.7	0.9	335
1988	R	200	73	282	365	28	9.0	0.8	285
	T	216	93	312	430	22	9.5	0.9	374
1989	R	152	66	304	434	19	8.1	0.9	395
	T	224	124	338	552	23	12.7	0.7	369
1990	R	110	94	345	619	14	11.6	0.7	435
	T	225	134	347	595	23	13.6	0.8	595

[a]Includes fish completing two summers of growth. See Eaton et al. (1992) for confidence intervals.

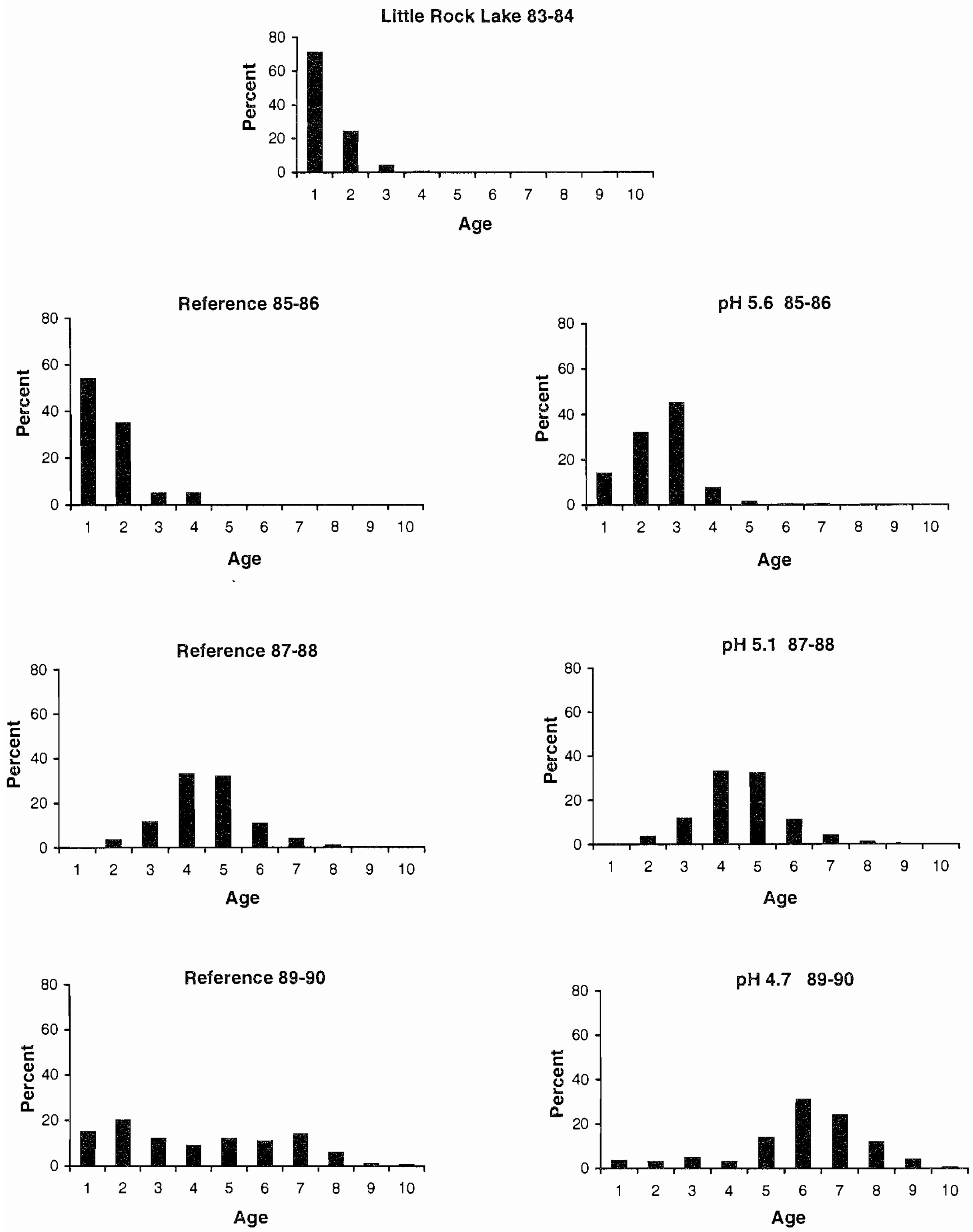

Figure 1. Age distribution of largemouth bass in Little Rock Lake during the pretreatment period (1983–1984), and in the R-basin and T-basin during the pH 5.6 treatment (85–87), pH 5.1 treatment (87–88), and pH 4.7 treatment (89–90).

11 times. An average of 63 percent were captured at least twice. Weight increment expressed as a function of initial weight illustrated the value of releasing smaller fish. For fish captured by all methods, weight during the first three captures more than doubled with each capture (r^2 = 0.51; P < 0.001). Weight gain did not increase significantly with additional captures (r^2 = 0.11; P > 0.2).

Nesting Activity and Success

Observers recorded the substrate composition for 91 percent of the 799 largemouth bass nests counted during this study (10 May–30 June, 1984–1990). The macrophyte *Myriophyllum tenellum* represented the primary substrate for 82 percent. The remaining nests were formed on some combination of logs, rock or gravel. Successful nests were guarded until the brood dispersed, an average of 15 days. Unsuccessful nests were guarded an average of three days (Table 2).

The number of nests formed each year was positively correlated (r = 0.88; P < 0.01) with the estimated number of potential spawners and averaged 0.49 nests per adult largemouth bass (Table 2). Differences between estimates for the R-basin (0.55) and T-basins (0.40) were not significant (t-test; P > 0.5). The small number of spawning adults and nests found in the reference basins during 1985 resulted from unequal division of the population when the lake was divided. Transfer of 33 age-1 and older bass and 691 young of year from the T-basin to the R-basin, during 1985, is partially responsible for the increased nesting activity observed in 1986 (Table 2). From 1987 to 1989 the number of nests in the R-basin continued to increase in response to the increased number of spawners. In the T-basin, peak spawner abundance and nesting activity occurred in 1987. After 1987 T-basin spawner abundance declined in response to lower recruitment (Table 2).

Yellow perch were observed preying upon largemouth bass embryos in nests. Predation on fry was not observed. The occurrence of yellow perch near nest sites and observed predation was highest during 1984, when the average weight of spawners was lowest (323 g). Snorkelers observed nest-guarding males "yawned" (stretching their jaws forward and apart in a wide gape, with opercles spread) upon being approached by a group of yellow perch. In most instances, the male would nip at the first few perch. When several perch attacked, the male moved off to the side and abandoned the nest. During the process of picking the embryos from the nests, most of the *Myriophyllum tenellum*, which formed the nest substrate, was uprooted. Both the direct observations of predation, and the uprooting of *Myriophyllum tenellum* were recorded in estimating nest predation rates. During 1984, 37 percent of the 41 nests were destroyed by predation, compared to 17 percent in the T-basin and 0 percent in the R-basin during 1989 when mean weight of spawners exceeded 600 g (Table 2). Nest predation appeared to decline with increased weight of spawners, but the relationship was not significant (r^2 = 0.38, P > 0.05). An inverse relationship between average

Table 2. Estimated spawner abundance and mean weight with nest number, predation loss, nesting success and duration of guarding (days) for Little Rock Lake (LRL) and the Reference (R) and Treatment (T) basins.

		Spawners		Nesting activity					
				Total	Nests/	Predation	Number	Duration	
Year	Basin	No.	Wt. (g)	No.	spawner	loss (%)	w/ fry (%)	w/ fry	w/o fry
1984	LRL	73	323	41	0.56	36	5	10	2
1985	R	10	536	3	0.30	66	0	–	2
	T	99	344	41	0.41	39	42	16	4
1986	R	76	345	44	0.58	20	9	21	4
	T	261	338	96	0.37	6	26	20	3
1987	R	57	450	33	0.58	18	12	9	4
	T	281	413	143	0.51	10	7	20	6
1988	R	104	540	58	0.55	3	24	13	4
	T	262	447	85	0.32	5	17	14	4
1989	R	115	653	57	0.50	0	30	16	3
	T	204	608	71[a]	N/A	17	0	–	3
1990	R	90	683	74	0.82	8	3	10	2
	T	205	627	53[a]	N/A	9	0	–	2

[a]Reduced observation schedule may have resulted in incomplete counts.

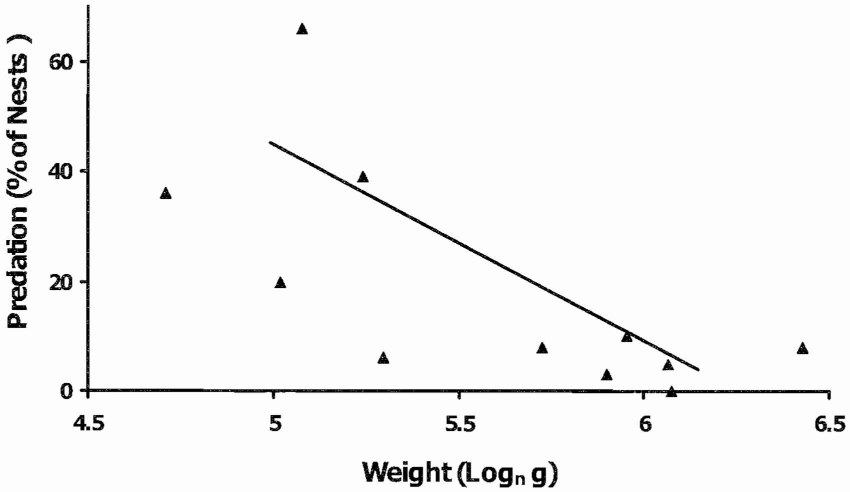

Figure 2. Relationship between the average weight (Naperian Log) of largemouth bass ≥ age 1 and nest predation. Estimates are for Little Rock Lake (1984), the R-basin (1985–1990), and the T-basin (1985–1988).

weight of age-1 and older largemouth bass and estimated predation rate was significant ($r^2 = 0.48$, $P < 0.05$; Figure 2).

Nesting success in the T-basin fell below the R-basin in 1987 and 1988, an apparent response to the pH 5.1 treatment (Table 2). During both years, a number of nests in the T-basin were observed with dead fry on the substrate. No nests were observed to produce swim-up fry at pH 4.7 (Table 2).

YOY Abundance, Growth, and Recruitment

Abundance of young of year increased significantly from 1983 to 1990 ($r^2 = 0.50$, $P < 0.01$), apparently reflecting the increased number of nests and nesting success rates (Figure 3). However, relationships between estimated YOY abundance, the estimated number or weight of spawners or the number of nests for the period 1984–1990, were not significant ($P > 0.05$).

Growth rates of young of year were greater in the R-basin than in the T-basin during 1985 through 1987 (ANCOVA; $P < 0.001$). Estimated mean TL 30 August did not appear to be dependent on YOY abundances or density ($r^2 = 0.2$; $P > 0.5$). However, recruitment (RI) increased significantly with YOY TL, estimated for the R-basin and for the T-basin through 1986 ($r^2 = 0.94$; $P < 0.01$). Young of year abundance and growth rates were higher during 1988 and appeared to result in stronger recruitment (Table 3).

The recruitment index (RI) indicated recruitment was highest early in the study when the number of spawners, nesting success, and August abundances of young of year were lower. Relative recruitment in both basins (T-basin 1985–1986) seemed to be strongly linked to largemouth bass biomass which was higher in the T-basin (Table 3). Recruitment (RI) was just as low for the 1985 year-class in the T-basin when biomass was 8.9 kg/ha and for the 1989 R-basin year-class when biomass was 8.1 kg/ha as it was in the T-basin during 1988 at pH 5.1. By assumming that biomass was similar during 1983 and 1984, the relationship between recruitment (RI) and biomass from 1983 through 1989 was described, based upon estimates not influenced by the pH 5.1 and 4.7 treatments or the higher young of year abundance and growth rates observed during 1988 (Figure 4). The analysis indicated recruitment declined significantly as biomass increased ($r^2 = 0.47$; $P < 0.05$).

Analysis of stomach content of largemouth bass collected after nesting was completed (Mid-July–October) indicated that cannibalism may influence recruitment. Stomachs of age-1 and older fish contained an average of 0.26 young of year. However, the intensity of cannibalism did not appear to be dependent upon YOY density ($r^2 = 0.12$; $P > 0.3$). The occurrence of cannibalism was significantly less in larger bass. Stomachs from fish greater than 300 mm averaged 0.15 young of year per individual, compared to 0.49 young of year in smaller individuals (t-test, $P < 0.01$). Diet analysis indicated larger bass shifted to feeding on yellow perch. Largemouth bass greater than 300 mm contained an average 0.6 yellow perch compared to 0.16 yellow perch in smaller bass (t-test, $P < 0.01$).

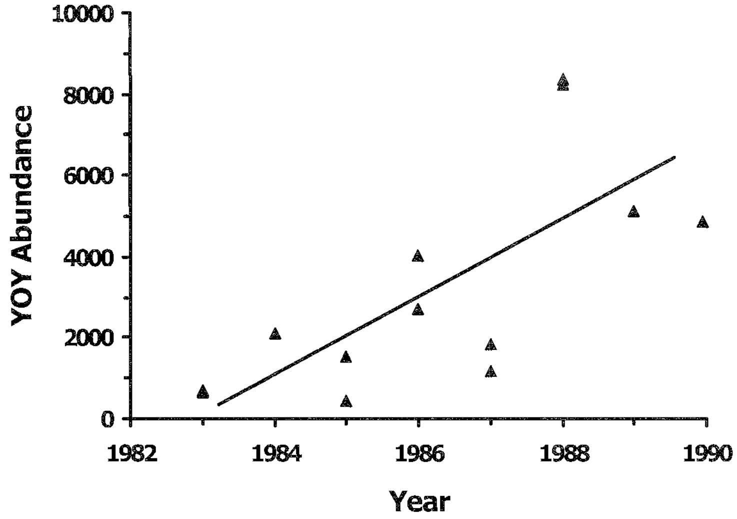

Figure 3. Changes in August abundance of YOY largemouth bass from 1993 to 1990.

Discussion

Age structure, low abundance and small size of spawners, the number of nests, and higher nest predation rates encountered early in this study all support a conclusion that Wisconsin's liberal fishing regulations in 1983 were not protecting largemouth bass populations in soft-water lakes like Little Rock Lake. These findings generally support the conclusion of Bennett et al. (1991), that protective regulations are needed to maintain large bass in northern populations.

Allen et al. (1998) suggest that natural and fishing mortality are additive in largemouth bass populations and protective regulations should directly reduce mortality. This study provides some support for that conclusion. However, limited sampling prior to the fishery closure reduced the precision of estimated average annual mortality during the creel fishery. The occurrence of two strong year-classes at the beginning of the study may have shifted age structure toward younger age classes,

Table 3. Largemouth bass August YOY abundance, estimated TL August 30, back-calculated Age 1 TL and recruitment index (RI) for Little Rock Lake (LRL) and the Reference (R) and treatment (T) basins.

		—Abundance—		———Growth TL (mm) ———			Recruitment index
Year	Basin	No.	(SE)	YOY (mm)	Age-1 (mm)	(SE)	Age 1
1983	LRL	1,360[a]			–	–	28
1984	LRL	4,200[a]			–	–	33[b]
1985	R	458[a]		79*	91	(8.5)	18
	T	1,518	(476)	68	87	(6.9)	1
1986	R	2,723	(475)	66*	72	(8.0)	15
	T	4,049	(658)	58	69	(9.6)	2
1987	R	1,172[a]		87*	92	(13.3)	39
	T	1,850[a]		76	75	(11.8)	0
1988	R	6,398	(551)	80	104	(16.9)	18
	T	8,231	(956)	82	119	(21.0)	8
1989	R	5,141	(451)	65	111	(17.5)	7
	T	0		--	125		1
1990	R	4,883	(901)				
	T	0					

*Indicates significantly longer than R-basin (ANCOVA; $P < 0.05$).
[a]No information for calculating standard error.
[b]Average for each basin (Total was 66 Age 1)

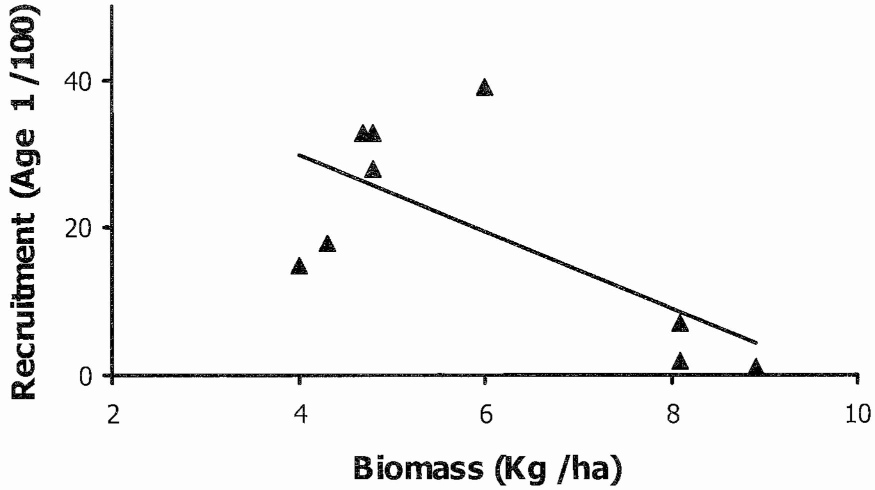

Figure 4. Relationship between largemouth bass biomass and relative recruitment (RI). Estimates are for Little Rock Lake (1983), the R-Basin (1984–1987, and 1989), and the T-Basin (1984–1986).

inflating the estimate. Otis et al. (1998) estimated total mortality of largemouth bass in Round Lake, Wisconsin, subject to similar fishing regulations to be 39 percent and 42 percent, during 1984 and 1985. Estimates of average annual mortality of 30 percent for the R-basin and 10 percent for the T-basin for the closure period and shifts in age structure suggest angling represented a major source of mortality. Beamesderfer and North (1995) reported average annual natural mortality for 49 Wisconsin largemouth bass populations to be 19 percent ($Z = 0.21$).

The number of spawners and nests increased significantly following the closure, as was predicted. Raffetto et al. (1990) found the number of male smallmouth bass breeding each year in another northern Wisconsin lake could be assumed to be the same as the number of nests containing eggs. My observations suggest that this is also probably true for largemouth bass. Both studies show that repeat spawning is uncommon. The instances when nest counts exceeded 50 percent of the estimated number of spawners can be explained by low precision of spawner abundance and population estimates.

One objective of the fishery closure was to reduce the number of variables limiting nesting success. The inverse relationship observed between average weight of largemouth bass and the intensity of nest predation suggests that predation was reduced. A similar relationship can be described between nest predation and the number of nests, indicating predator swamping may have been involved. However, yellow perch abundance estimates (age-2 and older; Eaton et al. 1992) indicate

Table 4. Number of YOY largemouth bass and yellow perch found in age-1 and older bass stomachs collected summer and fall 1985–1990 from the Reference (R) and Treatment (T) basins.

		Sample		Prey per sample	
Year	Basin	Total (No.)	Empty (%)	Bass (No.)	Perch (No.)
1985	R	45	49	0.06	0.00
	T	50	44	0.14	0.00
1986	R	25	40	0.40	0.00
	T	59	46	0.31	0.06
1987	R	25	48	0.15	0.32
	T	41	37	0.15	0.24
1988	R	22	23	0.23	0.59
	T	47	43	0.15	0.34
1989	R	21	43	0.57	0.38
1990	R	59	49	0.31	0.20

more than 200 age-2 and older yellow perch were present per nest, in both basins throughout this study. Clearly, enough predators existed to prey on all nests not effectively guarded. Nest observers also noted that larger guarding males were more aggressive towards them. Other studies demonstrate that mating success increases with male size (Philipp et al. 1997).

The decline in recruitment in response to increased largemouth bass biomass was not anticipated at the beginning of this study. A similar relationship was recently reported by Post et al. (1998). Both studies suggest that recruitment declines when largemouth bass biomass increases and that cannibalism functions as a compensatory mechanism that ultimately controls abundance and biomass. Positive relationships between YOY TL and recruitment have been identified in other studies (Garvey et al. 1998; Miranda and Hubbard 1994). Increased occurrence of yellow perch in the diet of largemouth bass greater than 300 mm suggests that shifts in size structure associated with the fishery closure also promoted increased predation by largemouth bass on a major nest predator. The long-term impacts of largemouth predation on yellow perch abundance and on largemouth bass recruitment should be positive.

Our angling catch rates reflected most of the changes in population demographics. Numerical catch rates did not increase; however, mean weight essentially doubled during the second and third captures. If quality of fishing is defined in terms of fish size, this study demonstrates that significant improvements result from catch-and-release regulations. Capture methods used in this study did not duplicate catch-and-release angling. However, hook-and-line sampling accounted for a high percentage of the capture, and handling mortality rates were similar to those reported for catch-and-release fishing (Kwak and Henry 1995; Hartley and Moring 1995).

Wisconsin bass fishing regulations have been modified three times since this project began. In 1889, a 305-mm (12 inches) size limit was introduced for waters in the northern half of Wisconsin. In 1992, bass fishing was restricted to catch and release until the third weekend in June, to protect nesting bass. During 1998, a statewide size limit of 356 mm (14 in) was introduced. Information generated during this study indicates that these regulations should benefit largemouth bass demographics and the quality of Wisconsin sport fisheries. The 1998 regulations would require release of 80 percent of the largemouth bass captured during this study and should improve population size structures and the quality of bass fishing. Under the present regulations, Little Rock Lake largemouth bass would be age-5 and older before entering the creel. Adults should have spawned several times and would be large enough to reduce nest predation by yellow perch. The influence on recruitment is less clear. The regulations may result in increased largemouth bass density and lower recruitment. Cannibalism was higher in size classes protected by the new regulations, but they do not protect larger bass that preyed primarily on yellow perch. These results indicate that slot-size limits may be more effective in managing for quality fishing.

Acknowledgments

T. Simonson, F. Stoll, B. Gobin, and R. Maslowski took responsibility for much of the field sampling and analysis. Their efforts are gratefully acknowledged. Logistical support for all Little Rock Lake research was provided through the University of Wisconsin Trout Lake Station and was critical to success of the research program. The study was supported largely by the U.S. Environmental Protection Agency through its Mid-Continent Ecology Division Laboratory in Duluth, Minnesota.

References

Allen, M. S., L. E. Miranda, and R. E. Brock. 1998. Implication of compensatory and additive mortality to the management of selected sportfish populations. Lakes and Reservoirs Research and Management 3:67–79.

Allen, R. C., and J. Romero. 1975. Underwater observations of largemouth bass spawning and survival in Lake Mead. Pages 104-112 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Barnhart, R. A. 1989. Symposium review: Catch and release fishing a decade of experience. North American Journal of Fishery Management 9:74–80.

Beamesderfer, R. C. P., and J. A. North. 1995. Growth, natural mortality and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North American Journal of Fishery Management 15:688–704.

Bennett, D. H., D. R. Hatch, and M. D. Liter. 1991. Managing largemouth bass in the northwest: a game of recruitment, protection, and patience. U.S. Forest Service Technical Report RM-207:313–322.

Brazonik, P. L., J. G. Eaton, T. M. Frost, P. J. Garrison, T. K. Kratz, C. E. Mach, J. H. McCormick, J. A.

Perry, W. A. Rose, C. J. Sampson, B. C. L. Shelley, W. A. Swenson, and K. E. Webster. 1993. Experimental Acidification of Little Rock Lake, Wisconsin: chemical and biological changes over the pH range 6.1 to 4.7. Canadian Journal of Fisheries and Aquatic Sciences 50:1101–1121.

Eaton J. G., W. A. Swenson, J. H. McCormick, T. D. Simonson, and K. M. Jensen. 1992. A field and laboratory investigation of acid effects on largemouth bass, rock bass, black crappie and yellow perch. Transactions of the American Fisheries Society 121:644–658.

Garvey J. E., W. A. Russel, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass *(Micropterus salmoides)*:Revisiting the role of body size. Canadian Journal of Fisheries and Aquatic Sciences 55:2414–2424.

Hartley, R. A., and J. R. Moring. 1995. Differences in mortality between largemouth and smallmouth bass caught in tournaments. North American Journal of Fishery Management 15:666–670.

Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Kwak, T. J., and M. G. Henry. 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. North American Journal of Fishery Management 15:621–630.

Miranda, L. E., and R. J. Muncy. 1987. Recruitment of young-of-the-year largemouth bass in relation to size structure of parental stock. North American Journal of Fishery Management 7:131–137.

Miranda, L. E., and W. D. Hubbard. 1994. Winter survival of age 0 largemouth bass relative to size, predators and shelter. North American Journal of Fisheries Management 14:790–796.

Otis, K. J., R. R. Piette, J. E. Keppler, and P. W. Rasmussen. 1998. A largemouth bass closed fishery to control an overabundant bluegill population in a Wisconsin lake. Journal of Freshwater Ecology 13:391–403.

Philipp, D. P. C. A. Toline, M. F. Kubacki, D. B. F. Philipp, and F. J. S. Phelan. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. North American Journal of Fishery Management 17:557–567.

Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality and the recruitment of largemouth bass in a northern lake. Canadian Journal of Fisheries and Aquatic Sciences 55:2588–2600.

Raffetto, N. S., J. R. Baylis, and S. L. Serns. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieu*). Ecology 71:1523–1535.

Rasmussen, J. L., and S. M. Michaelson. 1972. Attempts to prevent largemouth bass overharvest in three northwest Missouri lakes. Pages 69–83 *in* J.L. Funk, editor. Symposium on Overharvest and Management of Largemouth Bass in Small Impoundments. North Central Division, American Fisheries Society, Special Publication 3, Bethesda, Maryland.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin No. 191. Fisheries Research Board of Canada.

Swenson, W. A., and L. L. Smith Jr. 1993. Gastric digestion, food consumption, feeding periodicity and food conversion efficiency of walleye (*Stizostedion vitreum*). Journal of the Fisheries Research Board of Canada 30:1327–1336.

Swenson, W. A., W. P. Gobin, and T. D. Simonson. 1988. A calibrated mask-bar for underwater measurement of fish. North American Journal of Fisheries Management 8:382–385.

Watras, C. J., and T. M. Frost. 1989. Little Rock Lake: Perspectives on a experimental, ecosystem approach to seepage lake acidification. Archives of Environmental Contamination and Toxicology 18:157–165.

Welch, H. E., and K. H. Mills. 1981. Marking fish by scarring soft fin rays. Canadian Journal of Fisheries and Aquatic Sciences 38:1168–1170.