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Effects of catch-and-release angling on a largemouth bass (*Micropterus salmoides*) population in a north temperate lake, 2001–2005

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ABSTRACT

Catch-and-release associated mortality of largemouth bass (*Micropterus salmoides*; LMB) has received considerable attention due to the popularity of this fishery and the increasing prevalence of voluntary release by anglers. Most studies testing for the influences of catch-and-release fishing on LMB mortality and growth have been of short duration and conducted in artificial settings, which may or may not be representative of potential population-level responses observed in natural settings over longer time periods. We subjected Little Rock Lake South (8 ha), Vilas County, Wisconsin (closed to recreational angling) to an experimental five-year LMB catch-and-release fishery to test for effects on vulnerability to recapture, population abundance, size-structure, and growth. We fished Little Rock Lake South about once per week during May–September 2001–2005 with conventional angling gear and artificial lures. We also simulated or exceeded conditions typical of live-release tournaments by holding LMB after capture and later processing them for length, weight, and diet information. Catch-and-release mortality did not appear to negatively influence this LMB population as evidenced by the high number of recaptured individuals, increases in recruitment, and significant increase in density over time. We found no evidence of LMB being more difficult to recapture after being caught. Population size-structure decreased over time. Average body condition did not change over time; however, size-specific growth rates increased. The observed increase in growth rates, despite a significant increase in density, was likely associated with high prey availability. This increase may not be representative of growth effects observed over longer time scales should LMB density continue to increase. Our results suggest that catch-and-release fishing had minimal negative effects on the sustainability of an LMB population if greater abundances are desired. However, density-dependent compensatory responses in size-structure and growth may be expected over time.

1. Introduction

Catch-and-release fishing has become a popular practice for many recreational anglers and a tool for fisheries managers to increase fish abundances, angler catch rates, and trophy potential of fish stocks (Noble, 2002; Arlinghaus et al., 2007; Gaeta et al., 2013; Gilbert and Sass, 2016). The popularity of this practice for largemouth bass (*Micropterus salmoides*; LMB) anglers began during the 1990's, as more anglers began viewing LMB as a sportfish and the demand for the opportunity to catch more, larger LMB grew (Allen et al., 2008; Isermann et al., 2013; Hansen et al., 2015). Although previous studies have assessed catch-and-release mortality of LMB (Wilde, 1998; Neal and Lopez-Clayton, 2001; Allen et al., 2004; Edwards et al., 2004), most of these studies were performed using fish that had been captured only once during the study. In a 27-year mark-recapture study of LMB, Cline et al. (2012) found no long-term somatic growth responses to catch-and-release angling using barbless hooks. However, there is still a need to "assess angling encounter probabilities and the cumulative effects of multiple hookings" on LMB population dynamics (recapture rates, population abundance, size-structure, growth, mortality) over multiple years in a natural setting using conventional angling gear (including barbed single and treble hooks) (Bartholomew and Bohnsack, 2005). Further, Kerns et al. (2012) suggested the need to develop field studies to better understand the fishing mortality rate that occurs via catch-and-release angling.

Estimates of catch-and-release and tournament-associated mortality

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in LMB are highly variable (range 0–98%) and potentially biased due to confinement of bass in pens or cages following the catch-and-release or tournament weigh-in procedures (Schramm et al., 1987; Kwak and Henry, 1995; Weathers and Newman, 1997; Wilde, 1998; Pollock and Pine, 2007; Wilde and Pope, 2008). Holding fish in net pens only provides a measure of immediate (< 24 h) or short-term mortality (24–72 h) and does not allow for indirect mortality effects (i.e., predation) (Pollock and Pine, 2007). Thus, containment studies may not depict the true effects of catch-and-release or tournament fishing. Additional studies are needed that allow fish to be angled repeatedly under regular fishing conditions in order to test for population-level effects. For example, Jackson et al. (2015) found that catch-and-release angling for smallmouth bass (*Micropterus dolomieu*) in large lake systems had no population-level effects on recruitment and Trippel et al. (2017) showed that bed-fishing for Florida bass (*M. salmoides floridanus*) had no effect on recruitment or overall reproductive success.

Evaluations of catch-and-release fishing on LMB growth have also reached disparate conclusions. Pope and Wilde (2004) found no effect of catch-and-release fishing on LMB somatic growth during a 40-day study, but Siepker et al. (2006) noted a decrease in somatic growth in a 43-day study. Cline et al. (2012) observed about a six-day period of weight loss post-release, followed by a compensatory growth period back to normal weight.

Longer-term, ecosystem-scale studies may be required to better understand the consequences of catch-and-release fishing on LMB population dynamics. Such studies could provide critical information about determinants of changes in vulnerabilities of fishes following capture (Cox, 2000; van Poorten and Post, 2005). Cox (2000) proposed that fish may enter a "refractory state" where they are invulnerable to angling for some period following capture. However, van Poorten and Post (2005) suggested that the "refractory state hypothesis" of Cox (2000) could not adequately explain seasonal declines in rainbow trout (*Oncorhynchus mykiss*) CPUE and that other ecological or behavioral processes, other than the fishery, must be responsible. Rainbow trout CPUE declined with high angler effort, despite not harvesting any fish, suggesting some level of learned behavior in avoiding hooks (Askey et al., 2006).

We conducted a five-year study to test whether catch-and-release angling for LMB influenced catch-and-release mortality, simulated or stress-related tournament-associated mortality, vital rates (growth, mortality), and size-structure of the population. We used this long-term examination of a catch-and-release LMB fishery to test the "refractory state hypothesis" of Cox (2000), empirically quantify the range and variability in the "refractory state" of LMB following capture (if such a state exists), and to evaluate an ecological mechanism to explain differences in catchability of LMB.

2. Materials and methods

2.1. Study site

Little Rock Lake South (45°59′44.69"N, 89°42′12.76"W) is an 8 ha, oligotrophic, seepage lake in Vilas County, Wisconsin that has no lakeshore residential development (Sass et al., 2006). Little Rock Lake South was isolated from Little Rock Lake North (10 ha). Both basins were closed to public access and fishing during 1985–2007 (Swenson, 2002). The fish community of Little Rock Lake South was dominated by LMB and yellow perch (*Perca flavescens*), with rock bass (*Ambloplites rupestris*), black crappie (*Pomoxis nigromaculatus*), and central mudminnow (*Umbra limi*) present at low abundances.

2.2. Fish sampling

We angled LMB using conventional hook-and-line techniques about once per week during May – September 2001-2005. Only artificial lures (e.g. jigs, soft plastic grubs, plastic worms, spinnerbaits, crankbaits, stickbaits) with barbed hooks (single and treble) were used. Lure sizes ranged from a 76 mm long Berkley® power grub to a 133 mm Rapala® to avoid lure size bias associated with the sizes of the LMB captured (Wilde et al., 2003). During each angling event, we fished the entire shoreline of the lake from one or two boats for about 2–3 h. Catch rates were high and averaged five LMB/angler/hr (Sass, 2004). After capture, we placed each LMB in a 121 L tub filled with surface water from the lake for later processing. No mechanical aeration was provided to the tubs of water. Thus, our holding and later processing conditions likely exceeded what would be typical for live-release tournaments. When LMB showed early signs of stress (e.g., gulping at surface of water, slight loss of equilibrium), we drained ¾ of the water from the tub and replaced it with fresh lake water. Densities of LMB held in the tubs depended on daily catch and ranged from 1 to 30 fish/tub.

Upon completion of the angling event or when the tub was full, we measured each captured LMB for total length and weight. Fish ≥150 mm total length were marked with individually numbered t-bar Floy® tags, while fish < 150 mm received a specific fin clip. We also collected several scales from beneath the pectoral fin for age and growth determination. In a subset of the angled LMB, we determined diet composition by performing gastric lavage on up to 15 fish once every two weeks (Seaburg, 1957; Hodgson and Kitchell, 1987). We removed each LMB from oxygenated water for up to three minutes to collect growth and diet information. All LMB were released back to the lake following data collection.

2.3. Mark/recapture data

To quantify recapture rates, we compiled the total number of LMB captured and the total and individual number of recaptures for each LMB over the five-year period. We used a method similar to Ricker's (1975) estimation of survival from catch curves to determine recapture rates under two different scenarios: 1) the probability of recapturing a LMB t times given that it had been recaptured once; and 2) the probability of recapturing a LMB $t + 1$ times given that it has been recaptured t times. In scenario (1), we used mark-recapture data to calculate LMB recapture rates using the equation:

$$p(R) = \frac{N_t}{N_1} \tag{1}$$

where N_t is the total number of LMB recaptured t times, N_1 is the number of LMB recaptured once, and $p(R)$ represents the probability that a LMB is recaptured t times given that it has been recaptured once.

In scenario (2), we used the equation:

$$p(R) = \frac{N_{t+1}}{N_t} \tag{2}$$

where N_{t+1} is the total number of LMB recaptured $t + 1$ times, N_t is the total number of LMB recaptured t times, and $p(R)$ represents the probability that a LMB is recaptured $t + 1$ times given that it has been recaptured t times. We regressed the probability of recapture (N_{t+1}/N_t) (dependent variable) on recapture number (independent variable) to test for a relationship between recapture rates and the number of times a LMB was recaptured. Regression significance was determined by ANOVA ($\alpha = 0.05$) with a null hypothesis of no change in recapture rate with increasing number of recaptures. We also assessed the relationship between the number of times a LMB was recaptured and initial capture length. To estimate the refractory period after catch, we calculated the difference between time of capture and time of successive recapture for each LMB on an annual basis. We did not quantify the refractory period among seasons because we did not fish Little Rock Lake South from October to April in each year. We used a Chapman-modified, continuous Schnabel mark-recapture procedure (Ricker, 1975) to estimate annual LMB population densities using the equation:

$$N = \frac{\sum C_t M_t}{\sum R + 1} \tag{3}$$

where C_t = total sample taken on day t, M_t = total marked fish at large at the start of the t^{th} day, and R = total number of recaptures during the sampling period. The 95% confidence intervals for the population estimates were calculated using a Poisson distribution.

2.4. Size-structure

We calculated the proportional size distribution (PSD) for LMB annually based upon the length information collected during the mark-recapture population estimates (Gabelhouse, 1984; Neumann et al., 2012). Stock, quality, and preferred length for LMB was 200, 300, and 380 mm, respectively (Gabelhouse, 1984; Neumann et al., 2012). To test for the effects of catch-and-release fishing on PSD-Q and PSD-P, we used simple linear regression. We used the null hypothesis of no change in PSD over time at the $\alpha = 0.05$ level.

2.5. Largemouth bass growth

We examined body condition and size-specific growth rates to test for the effects of catch-and-release fishing on LMB growth. Body condition was estimated using relative weight for LMB (Wege and Anderson, 1978) and was calculated for all fish used for diet analysis because length and weight were recorded. The minimum total length used for the relative weight analysis was 150 mm (Wege and Anderson, 1978). We used simple linear regression to test for the effects of catch-and-releasing angling on average annual LMB body condition with the null hypothesis of no change in body condition over time ($\alpha = 0.05$).

Scales were analyzed to determine annual growth increments for different sizes of LMB. Our methods for determining size-specific growth rates and statistical analyses can be found in Schindler et al. (2000) and Sass et al. (2006). Size-specific growth rates provide greater statistical power than other indicators to detect effects of manipulations, such as our catch-and-release angling experiment (Carpenter et al., 1995). Annually, we collected scales from beneath the pectoral fin from five individual LMB for every available 10 mm increment of length (e.g. 100–109, 110–119 mm, etc.) captured. Scales were pressed between glass slides and photographed with a Polaroid DMC-2 digital camera. Scales were read using a Fishomatic optical imaging system developed by the Center for Limnology at the University of Wisconsin-Madison to determine an individual's growth increment in the previous year. Growth rate was determined by the Fraser-Lee method of back-calculating the length of the previous year using Carlander's constant of 20 mm for LMB (Carlander, 1982). We then regressed $\log_e$ growth rate (mm/yr, dependent variable) on fish length (mm, independent variable) for LMB annually to determine mean growth rates for four common length groups (100, 200, 300, 400 mm total length; Carlander, 1982; Schindler et al., 2000; Sass et al., 2006). Only one size-specific growth rate was calculated from each individual fish. We used simple linear regression to test for the effects of catch-and-releasing angling on LMB size-specific growth rates with the null hypothesis of no change in size-specific growth rates over time ($\alpha = 0.05$).

2.6. Largemouth bass mortality rates

Because population estimates were conducted annually in 2001–2004, we calculated the finite annual mortality rate between successive age classes in 2001–2002, 2002–2003, and 2003–2004. We calculated the finite annual mortality rate as:

$$p(A) = 1 - \frac{N_{t+1}}{N_t}$$

where A is the finite annual mortality rate, N_t is the number of LMB in each cohort at time t, and N_{t+1} is the number of LMB in each cohort at time $t + 1$ (Ricker, 1975). This mortality rate was a function of natural mortality and catch-and-release fishing mortality because no harvest was allowed in this system during our study. Mortality rates were calculated for each age class where N_{t+1} was less than N_t in 2001–2004 based upon the population estimates.

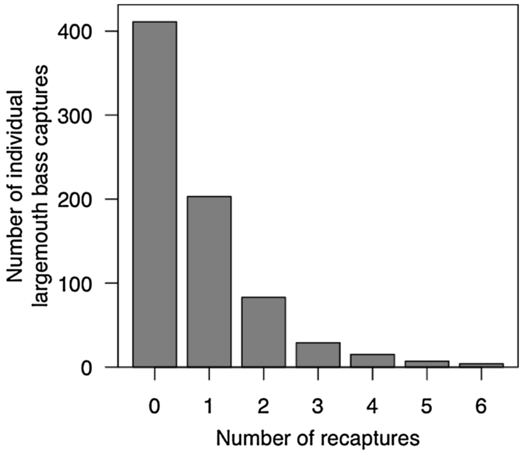

Fig. 1. Recapture frequency distribution for largemouth bass (*Micropterus salmoides*) captured in Little Rock Lake South, Wisconsin during 2001–2005.

3. Results

3.1. Mark/recapture data

A total of 752 individual LMB were captured by hook-and-line angling from Little Rock Lake South and the lake was fished once every 7.5 ± 0.88 days during 2001–2005. Of that total, 27% (n = 203) of the LMB were recaptured at least once (Fig. 1). The maximum number of times an individual LMB was recaptured was six (n = 4). The number of times an individual LMB was recaptured decreased exponentially (Fig. 1). The probability of a LMB being recaptured a second time was about 39%, while the probability of recapturing a bass six times was just over 1% during the five year study (Fig. 1). The probability of a LMB being recaptured N_{t+1} times after being captured N_t times was relatively consistent and ranged from about 35–53% during the study. No statistically significant difference was found in the probability of a LMB being captured N_{t+1} times given that it had been captured N_t times ($p > 0.05$).

Fish length and days at large influenced recapture probability. The number of times an individual LMB was recaptured was positively correlated with length at initial capture (Fig. 2), indicating that fish vulnerability to angling increased with length. The average annual refractory period between capture and recapture for individual LMB was about 35 days. Minimum and maximum refractory periods for LMB were 0 and 116 days. The average refractory period for individual LMB did not change among years ($p > 0.05$). Based on the population estimates, about 25–53% of the LMB population was captured annually during 2001–2005 (Fig. 3). The percentage of the LMB population captured annually did not change over time (Fig. 3) ($p > 0.05$). Densities of LMB in Little Rock Lake South increased from 2001 to 2005 (Fig. 4). Based on the lack of overlap of the 95% confidence intervals, LMB density was significantly greater in 2004 and 2005 compared to 2001 and 2002 (Fig. 4).

3.2. Size-structure

The size-structure of the LMB population in Little Rock Lake South declined from 2001 to 2005. The PSD-Q of the LMB population decreased significantly over time from about 75% in 2001 to 29% in 2005 ($n = 5$, $df = 1,3$, $f = 42.83$, $p = 0.007$, $r^2 = 0.91$) (Fig. 5). The PSD-P

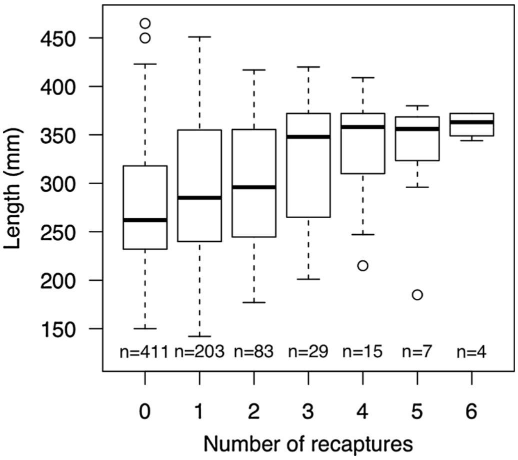

Fig. 2. The number of times largemouth bass (*Micropterus salmoides*) were recaptured versus initial capture length in Little Rock Lake South, Wisconsin during 2001–2005. Box plots are shown with medians, first and third quantiles, and a range of 1.5 times the interquantile range. Outliers beyond the range are represented as open circles.

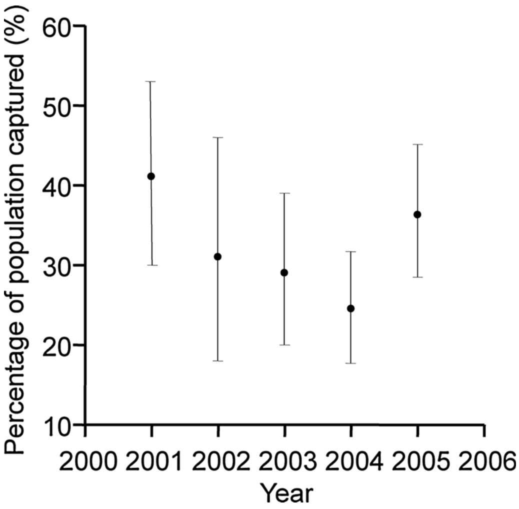

Fig. 3. Scatterplot of the proportion of the largemouth bass (*Micropterus salmoides*) population captured in Little Rock Lake South, Wisconsin during 2001–2005. Error bars represent the 95% confidence intervals about the estimate.

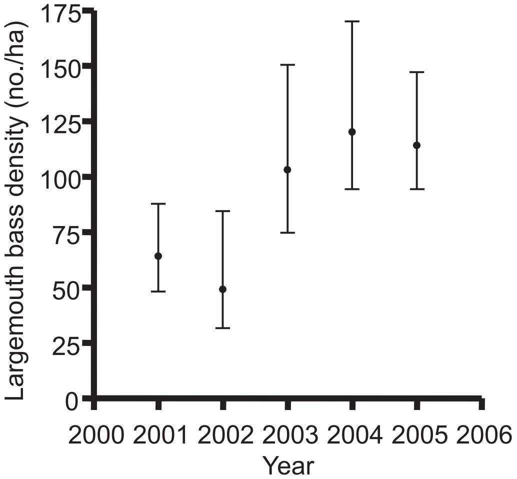

Fig. 4. Scatterplot of the density (no./ha) of largemouth bass (*Micropterus salmoides*) in Little Rock Lake South, Wisconsin during 2001–2005. Errors bars represent the 95% confidence intervals about the estimate.

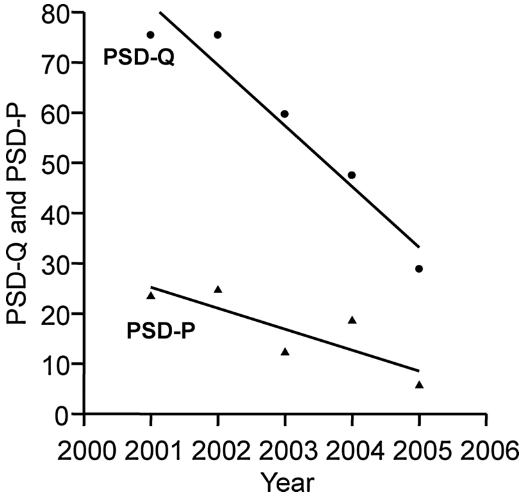

Fig. 5. Proportional size distribution (PSD-Q, PSD-P) of the largemouth bass (*Micropterus salmoides*) population in Little Rock Lake South, Wisconsin during 2001–2005.

also decreased from about 23% to 6% during 2001 and 2005, respectively. Decline in PSD-P was not statistically significant ($n = 5$, df = 1,3, $f = 6.5$, $p = 0.084$, $r^2 = 0.58$) (Fig. 5).

3.3. Growth

Average body condition of the LMB population did not change, while growth rates of two length groups increased during 2001–2005. Average relative weight of the LMB population remained in the low- to mid-80% range (82–86%) throughout the study ($p > 0.05$). Size-specific growth rates of the two smallest length groups of LMB (100, 200 mm) did not change over time. Size-specific growth rates of the 300 and 400 mm length groups increased significantly from 2001 to 2004 (300 mm, $n = 4$, df = 1,2, $f = 113.9$, $p = 0.009$, $r^2 = 0.974$; 400 mm, $n = 4$, df = 1,2, $f = 31.59$, $p = 0.03$, $r^2 = 0.91$) (Fig. 6). Size-specific growth rates increased by about 10–15 mm/yr for the 400 and 300 mm length groups of LMB, respectively.

3.4. Mortality rates

Mortality rates among all age classes were variable from 2001 to 2004 (Fig. 7). The average annual mortality rate among all age classes in 2001–2004 was about 43%. Average mortality rates for age-2-9 LMB were about 33%. Average mortality rates for ≥age-10 LMB were about

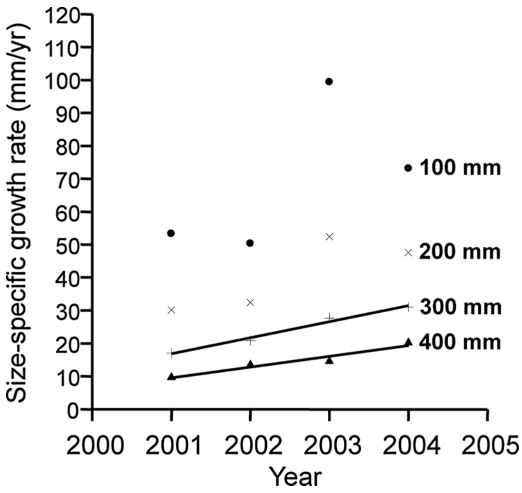

Fig. 6. Size-specific growth rates for four common length groups of largemouth bass (*Micropterus salmoides*) in Little Rock Lake South, Wisconsin during 2001–2004.

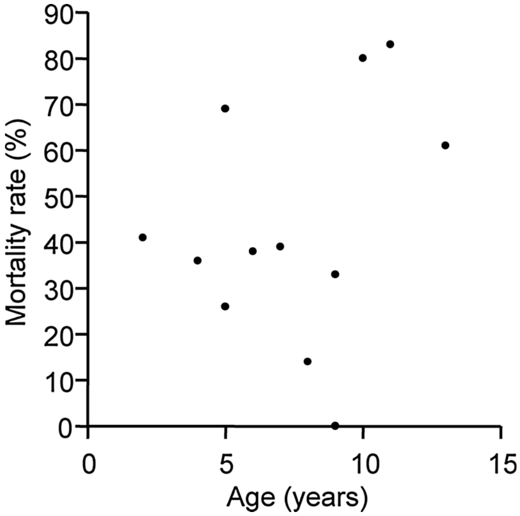

Fig. 7. Scatterplot of largemouth bass (*Micropterus salmoides*) mortality rate versus age in Little Rock Lake South, Wisconsin from 2001 to 2004.

75% from 2001 to 2004.

4. Discussion

4.1. General trends

Our study was novel in its duration (but see Cline et al., 2012), control, natural setting, and the number of variables examined to test for potential responses to catch-and-release angling compared to previous micro- and mesocosm studies that encompassed relatively shorter time scales. We subjected Little Rock Lake South to five years of catch-and-release LMB fishing, which also simulated or exceeded some conditions typical of LMB tournament holding and weigh-in procedures (e.g., holding, length and weight measurements, scale extraction, gastric lavage). Our fishing effort/ha was similar to average fishing effort in open access Florida lakes (Micheal S. Allen, University of Florida, unpublished data), suggesting that we experimentally obtained a realistic level of recreational angling effort for LMB. Average Florida bass angling effort on 16 Florida lakes was about 3.1 h/ha/100 days (Micheal S. Allen, University of Florida, unpublished data) and our average angling effort was about 5.0 h/ha/100 days during the study. Experimentally subjecting Little Rock Lake South to recreational catch-and-release angling at this level of effort did not appear to negatively influence this LMB population as evidenced by the high number of recaptured individuals, increase in recruitment, and significant increase in density over time. Further, our mean total mortality estimate (43%) was similar to natural mortality estimates for Florida, largemouth, and smallmouth bass (29–46%) suggesting that catch-and-release mortality was low (0–14%) and within the range of rates observed for Florida bass (3–7%) (Beamsderfer and North, 1995; Waters et al., 2005; Kerns et al., 2016). Catch-and-release mortality was likely negligible for age-2-9 LMB (total mortality = 33%), whereas it may have been greater for LMB ≥ age-10 (total mortality = 75%) and/or natural mortality rates may have been greater in these older age classes. If catch-and-release mortality were a significant factor influencing population responses, we would have expected a decline in PSD-Q, PSD-P, and LMB density over time. We observed a decline in PSD-Q and PSD-P, but a significant increase in LMB density; all three trends suggest greater levels of recruitment into the population and relatively low catch-and-release mortality. However, we cannot fully discount some higher level of catch-and-release fishing mortality upon initial older, dominant cohorts, which may have shifted the size-structure from a less dense population with larger fish to a more robust population with smaller fish (Hansen et al., 2015). Our results suggest that an increase in population size may be paralleled by an increase in competition, which may make larger LMB competitively superior and more vulnerable to hook-and-line angling as a consequence of energetic requirements and size-structured interactions (Hodgson and Kitchell, 1987). Increased vulnerability of larger LMB in our study was emphasized by the positive relationship observed between the number of times a LMB was recaptured and its initial length at capture and size-specific effects on growth of larger individuals. Our results also suggest that “short-term studies”, such as the 40-day catch-and-release study by Pope and Wilde (2004) and the 43-day study of Siepker et al. (2006), may be insufficient in duration to adequately assess the responses of LMB populations to catch-and-release angling.

4.2. Bass recapture trends and vulnerability

The probability of recapturing a LMB *t* times given that it was recaptured once decreased exponentially with increasing number of recaptures. This observation likely relates to our inability to capture all LMB in Little Rock Lake South on an annual basis due to determinate, yet consistent, amounts of angling effort and a likely refractory period after capture (~35 days in our study). Our inability to recapture all LMB in the system prevented complete confirmation that catch-and-release angling resulted in negligible hooking mortality. However, significant increases in LMB density and recruitment, and the high number of LMB recaptured more than once over multiple years (≤6 times over 5 years) suggests a minimal effect of catch-and-release mortality using standard angling techniques. Similar negligible effects of catch-and-release fishing have been observed by Mankin et al. (1981), Quinn (1989), Pope and Wilde (2004), and Cline et al. (2012). Our results indicate that the process of a LMB being hooked, played, handled, held in a livewell, and released multiple times does not cause significant mortality and provides evidence for catch-and-release angling as a productive fisheries management practice for increasing LMB densities similar to the findings of Jackson et al. (2015) for smallmouth bass and Trippel et al. (2017) for Florida bass. Further supporting our conclusions, Cline et al. (2012) recaptured individual LMB up to six times during a given season and recaptured a single LMB 22 times over a 27 year period. Our results also suggest that LMB tournament-associated delayed mortality may be biased when fish are held in enclosures and not returned immediately to the waterbody unhindered (Schramm et al., 1987; Kwak and Henry, 1995; Weathers and Newman, 1997; Neal and Lopez-Clayton, 2001). Indeed, Wilde and Pope (2008) reported that survivorship of LMB that were hand-hooked within the oral cavity and esophagus across a range of water temperatures was 98 and 55%, respectively. The Wilde and Pope (2008) study was carried out in a laboratory setting and may not completely simulate what habitat conditions LMB may choose in an open system following capture and release, thus survivorship could be even greater as evidenced by Kerns et al. (2016) (93–97% survivorship) for Florida bass.

In contrast to our findings above, individual vulnerabilities of LMB captured *t + 1* times given that they were captured *t* times remained relatively constant (~0.44) over all number of recaptures. Additionally, length was positively related to the number of recaptures. Cox (2000) proposed that fish in open-access fisheries were present in one of three states: (1) fish that are either too small to react to lures or are present in areas that are not being fished; (2) fish that are reactive to fishing gear and are available to be caught; and (3) fish that have been caught and released, but are then unavailable to be caught because of a behavioral shift after release, known as a refractory state. Our study system and experimental design discounts LMB existing in state (1) because Little Rock Lake South is small and could be fished entirely during each sampling event and a large range of lure-sizes and types were used to avoid lure-size constraints on catchability in the population (Wilde et al., 2003). All LMB in our study, except for young-of-the-year, were assumed to be vulnerable to angling or in a refractory state after catch. Our observed refractory periods (0–116 days) were similar to those reported by Cline et al. (2012) (1–98 days).

Largemouth bass recaptured a greater number of times in our study tended to be longer individuals at initial capture. Our results are similar to those of Mankin et al. (1981) and Burkett et al. (1986) who found greater vulnerabilities of longer LMB to angling. Mankin et al. (1981) attributed this finding to increased competition among longer individuals for limiting food resources.

4.3. Largemouth bass population dynamics

Size-structure of the LMB population decreased in Little Rock Lake South during our five-year study as evidenced by PSD-Q and PSD-P values. Our results indicated that a catch-and-release LMB fishery with relatively low incidences of hooking mortality resulted in increased abundance and smaller size-structure (Backiel and Le Cren, 1967; Mankin et al., 1981). Therefore, the expected long-term result of catch-and-release LMB fishing may be manifested in the decline of preferred, quality, and trophy size fish within a population, yet increased overall abundances and catch rates. Indeed, long-term analyses of Wisconsin LMB populations showed significant increases in relative abundances and recreational angler catch rates over time under a catch-and-release-only season during the spawning period, a minimum length limit of 356 mm, and a daily bag limit of five during 1990–2011 (Hansen et al., 2015; Rypel et al., 2016). Further, the mean length of age-6 LMB declined significantly over this same time period (Hansen et al., 2015). The decrease in size-structure observed in our study was likely related to improvements in LMB recruitment, mortality of initial, older dominant cohorts remaining from the complete fishery closure, and a minimal amount of catch-and-release mortality.

In contrast to previous studies (Post et al., 1999; Diana et al., 1991; Sass et al., 2004; Sass and Kitchell, 2005), the increase in LMB density observed in our study did not result in density-dependent constraints on growth. Largemouth bass body condition did not change over time. Size-specific growth rates increased from 2001 to 2004 and growth rates of the 300 and 400 mm length groups of LMB increased significantly. The lack of an influence of catch-and-release fishing on LMB body condition in our study supported the conclusions of Pope and Wilde (2004) and Cline et al. (2012), but contrasted the findings of Siepker et al. (2006) who predicted and empirically reported somatic weight loss of captured and released LMB compared to controls. A recent long-term study of Wisconsin LMB populations showed that growth was density-dependent and declined under conditions of increasing LMB relative abundances and recreational angler voluntary release rates (Hansen et al., 2015).

The short-term growth responses of LMB observed within our study may be related to forage availability. Increases in the density of yellow perch in Little Rock Lake South during 2001–2004 may best explain the observed patterns in LMB growth rates over time and the lack of density-dependence observed (Sass, 2004). Yellow perch densities in Little Rock Lake South were 696, 636, and 1230/ha in 2001, 2002, and 2004, respectively (Sass, 2004). Over this time period, yellow perch averaged about 72% of the dry mass proportion of LMB diets (Sass, 2004; Sass et al., 2006). Significant increases in the size-specific growth rates of the 300 and 400 mm length groups compared to the smaller length groups may have been a result of size-specific competitive advantages in larger LMB and gape limitation in smaller LMB. Our results suggest that the catch-and-release fishery had little negative effect on LMB growth and that the availability of yellow perch may have been an important driver of this response. However, we caution that density-dependent effects on the growth rates of LMB may not be dampened indefinitely in a primarily catch-and-release fishery (Hansen et al., 2015). Density-dependent constraints on LMB growth may have become evident if our catch-and-release fishery had continued, LMB density continued to increase, and yellow perch abundance decreased due to predation and other ecosystem changes, such as drought and associated lake level decline (Gaeta et al., 2014).

The annual total mortality rates we observed in this fishery were not suggestive of a major catch-and-release mortality effect similar to previous laboratory and field studies (e.g. Wilde and Pope, 2008; Kerns et al., 2016). In addition to some minimal catch-and-release mortality, increases in mortality rates of larger LMB were likely due to mortality of older individuals remaining from the total fishery closure during 1984–2000. Our average total mortality rates were within the range (24–91%) of annual LMB and Florida bass mortality rates reported by Allen et al. (2008) and Kerns et al. (2016). The LMB natural mortality rate of 31% reported by Waters et al. (2005) and 29–46% reported by Kerns et al. (2016) for Florida bass were not widely different from our average estimates of total mortality for all age classes (~43%) and LMB ages 2–9 (~33%), further suggesting minimal catch-and-release mortality. Our observed increase in LMB density over time, as a result of improved recruitment, and our estimated total mortality rates suggest that our catch-and-release fishery had minimal effects on this LMB population.

4.4. Conclusions

When LMB are the top piscivore in north temperate lakes, assessments should be made in regard to the type of fishery desired when considering catch-and-release as a management option. Our results indicate that a catch-and-release policy (and/or increasing rates of voluntary release; Allen et al., 2008; Gaeta et al., 2013; Isermann et al., 2013; Hansen et al., 2015) will likely result in increased abundances of LMB, but decreases in the size-structure of the populations and subsequent trophy fish potential (Rypel et al., 2016). Similar results have been observed for smallmouth bass (Jackson et al., 2015). Effects of a catch-and-release fishery on LMB growth may or may not become evident immediately and will likely be determined in the longer-term by interactions among density-independent factors (e.g., lake productivity, water temperature, prey availability) and density-dependent factors. Because catch-and-release mortality was minimal and there has been a long-term trend in voluntary angler release of LMB (Allen et al., 2008; Gaeta et al., 2013; Isermann et al., 2013), we predict that long-term catch-and-release policies will ultimately result in a fishery where LMB will be subject to density-dependent constraints on growth (Hansen et al., 2015; Rypel et al., 2016). If fisheries managers desire elevated numbers and catch rates of smaller LMB, a catch-and-release fishery and promoting voluntary angler release would be appropriate. If fisheries managers desire to optimize catch rates, growth and trophy potential, and maintain a sustainable LMB population, some level of harvest and/or a maximum length limit may be required.

We do not recommend extrapolating our findings in a five year catch-and-release study to systems where nesting LMB are not protected from the fishery. We did not specifically target nesting LMB, although some spawning males were captured in our study. This practice, whether it be catch-and-release or for harvest, and the presence of brood predators in a system could result in differing outcomes to this management strategy since angling of nesting bass has been shown to negatively affect individual reproductive success (Kieffer et al., 1995; Ostrand et al., 2004; Suski and Philipp, 2004; Trippel et al., 2017). Nevertheless, Jackson et al. (2015) and Trippel et al. (2017) showed no negative population level responses as a result of catch-and-release angling for nesting smallmouth and Florida bass, respectively. The long-term practice of targeting nesting LMB in a catch-and-release fishery might restrict population growth, make modeled harvest estimates inappropriate, and result in a low abundance LMB fishery. At the same time, long-term catch-and-release angling only during the LMB spawning season in northern Wisconsin did not result in any negative population growth effects (Hansen et al., 2015).

Our study also has implications for live release LMB tournaments. In our study, angling, handling, retention of bass in oxygenated water for up to three hours, and the collection of length, weight, and diet information had minimal effects on LMB mortality rates and refractory periods. Our study does suggest that the refractory period in LMB may be quite short following capture; however, the refractory periods observed in this study may be strongly influenced by the high densities of LMB in the study system and the level of competition for limiting resources (Cline et al., 2012). During a typical tournament day, LMB may be confined in livewells for eight hours or more. This holding period places considerable physiological stress on LMB, particularly if culling is not allowed (Suski et al., 2005). Our results suggest that delayed catch-and-release mortality rates can be greatly reduced if LMB are released unconfined within three hours of capture. Given the exposure and popularity of bass tournaments, catch-and-release mortality rates may be reduced by requiring weigh-in by officials at various portions of the lake during tournaments similar to what is currently being done in live-release muskellunge (*Esox masquinongy*) tournaments.

We conclude that some level of harvest may be required to balance and optimize LMB population sustainability, angler catch rates, and growth depending upon the management goals of the fishery. Within LMB management plans, managers must also consider species-specific angler behaviors (e.g. harvest-oriented versus voluntary release) in regards to predicted outcomes. We recommend that future research experimentally test for long-term population-level effects of closed, catch-and-release-only, and open fishery seasons upon nesting bass at an ecosystem-scale across the range of black basses.

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References

Allen, M.S., Rogers, M.W., Myers, R.A., Bivin, W.M., 2004. Simulated impacts of tournament associated mortality on largemouth bass fisheries. North Am. J. Fish. Manag. 24, 1252–1265.

Allen, M.S., Walters, C.J., Myers, R., 2008. Temporal trends in largemouth bass mortality, with fishery implications. North Am. J. Fish. Manag. 28, 418–427.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., Thorstad, E.B., 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev. Fish. Sci. 15, 75–167.

Askey, P.J., Richards, S.A., Post, J.R., Parkinson, E.A., 2006. Linking angler catch rates and fish learning under catch-and-release regulations. North Am. J. Fish. Manag. 26, 1020–1029.

Backiel, T., Le Cren, E.D., 1967. Some density relationships for fish population parameters. In: Gerring, S.D. (Ed.), The Biological Basis of Freshwater Fish Production. John Wiley and Sons, pp. 261–293.

Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. 15, 129–154.

Beamsderfer, R.C.P., North, J.A., 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North Am. J. Fish. Manag. 15, 688–704.

Burkett, D.P., Mankin, P.C., Lewis, G.W., Childers, W.F., Philipp, D.P., 1986. Hook-and-line vulnerability and multiple recapture of largemouth bass under a minimum total-length limit of 457 mm. North Am. J. Fish. Manag. 6, 109–112.

Carlander, K.D., 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. Trans. Am. Fish. Soc. 111, 332–336.

Carpenter, S.R., Cunningham, P., Gafny, S., Munoz-Del-Rio, A., Nibbelink, N., Olsen, M., Pellett, T., Storlie, C., Trebitz, A., 1995. Response of bluegill to habitat manipulations:power to detect effects. North Am. J. Fish. Manag. 15, 519–527.

Cline, T.J., Weidel, B.C., Kitchell, J.F., Hodgson, J.R., 2012. Growth response of largemouth bass (*Micropterus salmoides*) to catch-and-release angling: a 27-year mark-recapture study. Can. J. Fish. Aquat. Sci. 69, 224–230.

Cox, S., 2000. Angling Quality, Effort Response, and Exploitation in Recreational Fisheries: Field and Modeling Studies of British Columbia Rainbow Trout (*Oncorhynchus mykiss*) Lakes. University of British Columbia, Vancouver (Doctoral dissertation).

Diana, J.S., Dettweiler, D.J., Lin, C.K., 1991. Effect of Nile tilapia (*Oreochromis niloticus*) on the ecosystem of aquaculture ponds, and its significance to the trophic cascade hypothesis. Can. J. Fish. Aquat. Sci. 48, 183–190.

Edwards, G.P., Neumann, R.M., Jacobs, R.P., Odonnell, E.B., 2004. Impact of small club tournaments on black bass populations in Connecticut and the effects of regulation exemptions. North Am. J. Fish. Manag. 24, 811–821.

Gabelhouse Jr., D.W., 1984. A length-categorization system to assess fish stocks. North Am. J. Fish. Manag. 4, 273–285.

Gaeta, J.W., Beardmore, B., Latzka, A.W., Provencher, B., Carpenter, S.R., 2013. Catch-and-release rates of sport fishes in northern Wisconsin from an angler diarysurvey. North Am. J. Fish. Manag. 33, 344–350.

Gaeta, J.W., Sass, G.G., Carpenter, S.R., 2014. Drought-driven lake level loss: effects on coarse woody habitat and fish. Can. J. Fish. Aquat. Sci. 71, 1–11.

Gilbert, S.J., Sass, G.G., 2016. Trends in a northern Wisconsin muskellunge fishery: results from a county-wide angling contest, 1964–2010. Fish. Manag. Ecol. 23, 172–176.

Hansen, J.F., Sass, G.G., Gaeta, J.W., Hansen, G.J.A., Isermann, D.A., Lyons, J., Vander Zanden, M.J., 2015. Largemouth bass management in Wisconsin: intra- and inter-specific implications of abundance increases. In: In: Tringali, M.D., Long, J.M., Birdsong, T.W., Allen, M.S. (Eds.), Black Bass Diversity: Multidisciplinary Science for Conservation. Am. Fish. Soc. Symp., vol. 82. pp. 193–206.

Hodgson, J.R., Kitchell, J.F., 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). Am. Midl. Nat. 118, 323–336.

Isermann, D.A., Maxwell, J.B., McInerny, M.C., 2013. Temporal and regional trends in black bass release rates in Minnesota. North Am. J. Fish. Manag. 33, 344–350.

Jackson, J.R., Einhouse, D.W., VanDeValk, A.J., Brooking, T.E., 2015. Year-class production of black bass before and after opening of a spring catch-and-release season in New York: case studies from three lakes. In: In: Tringali, M.D., Long, J.M., Birdsong, T.W., Allen, M.S. (Eds.), Black Bass Diversity: Multidisciplinary Science for Conservation. Am. Fish. Soc. Symp., vol. 82. pp. 181–191.

Kerns, J.A., Allen, M.S., Harris, J.E., 2012. Importance for assessing population-level impact of catch-and-release mortality. Fisheries 37, 502–503.

Kerns, J.A., Allen, M.S., Hightower, J., 2016. Components of mortality within a black bass high release recreational fishery. Trans. Am. Fish. Soc. 145, 578–588.

Kieffer, J.D., Kubacki, M.R., Phelan, F.J.S., Philipp, D.P., Tufts, B.L., 1995. Effects of catch and-release angling on nesting male smallmouth bass. Trans. Am. Fish. Soc. 124, 70–76.

Kwak, T.J., Henry, M.G., 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. North Am. J. Fish. Manag. 15, 621–630.

Mankin, P.C., Burkett, D.P., Beaty, P.R., Childers, W.F., Philipp, D.P., 1981. Effects of population density and fishing pressure on hook-and-line vulnerability of largemouth bass. Trans. Ill. Acad. Sci. 77, 229–240.

Neal, J.W., Lopez-Clayton, D., 2001. Mortality of largemouth bass during catch-and release tournaments in a Puerto Rico reservoir. North Am. J. Fish. Manag. 21, 834–842.

Neumann, R.M., Guy, C.S., Willis, D.W., 2012. Length, weight, and associated indices. In: Zale, A.V., Parrish, D.L., Sutton, T.M. (Eds.), Fisheries Techniques, 3rd edition. Am. Fish. Soc., Bethesda, Maryland, pp. 637–676.

Noble, R.L., 2002. Reflections on 25 years of progress in black bass management. In: In: Phillipp, D.P., Riggway, M.S. (Eds.), Black Bass: Ecology, Conservation, and Management. Am. Fish. Soc. Symp., vol. 31. pp. 419–431.

Ostrand, K.G., Cooke, S.J., Wahl, D.H., 2004. Effects of stress on largemouth bass reproduction. North Am. J. Fish. Manag. 24, 1038–1045.

Pollock, K.H., Pine III, W.E., 2007. The design and analysis of field studies to estimate catch-and-release mortality. Fish. Manag. Ecol. 14, 123–130.

Pope, K.L., Wilde, G.R., 2004. Effect of catch-and-release angling on growth of largemouth bass, *Micropterus salmoides*. Fish. Manag. Ecol. 11, 39–44.

Post, J.R., Parkinson, E.A., Johnson, N.T., 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. Ecol. Monogr. 69, 155–175.

Quinn, S.P., 1989. Recapture rates of voluntarily released largemouth bass. North Am. J. Fish. Manag. 9, 86–91.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191.

Rypel, A.L., Lyons, J., Tober Griffin, J.D., Simonson, T.D., 2016. Seventy-year retrospective on size-structure changes in the recreational fisheries of Wisconsin. Fisheries 41, 230–243.

Sass, G.G., Kitchell, J.F., 2005. Can growth be used as a surrogate measure of walleye (*Sander vitreus*) abundance change? Can. J. Fish. Aquat. Sci. 62, 2159–2168.

Sass, G.G., Hewett, S.W., Beard Jr., T.D., Fayram, A.H., Kitchell, J.F., 2004. The role of density-dependence in growth patterns of ceded territory walleye populations of northern Wisconsin: effects of changing management regimes. North Am. J. Fish. Manag. 24, 1252–1265.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E., Turner, M.G., 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Fisheries 31, 321–330.

Sass, G.G., 2004. Fish Community and Food Web Responses to a Whole-Lake Removal of Coarse Woody Habitat. University of Wisconsin-Madison (Ph.D. thesis).

Schindler, D.E., Geib, S.I., Williams, M.R., 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems 3, 229–237.

Schramm Jr., H.L., Haydt, P.J., Portier, K.M., 1987. Evaluation of prerelease, postrelease, and total mortality of largemouth bass caught during tournaments in two Florida lakes. North Am. J. Fish. Manag. 7, 394–402.

Seaburg, K.G., 1957. A stomach sampler for live fish. Prog. Fish. Cult. 19, 137–139.

Siepker, M.J., Ostrand, K.G., Wahl, D.H., 2006. Effects of angling on feeding by largemouth bass. J. Fish Biol. 69, 783–793.

Suski, C.D., Philipp, D.P., 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. Trans. Am. Fish. Soc. 133, 1100–1106.

Suski, C.D., Cooke, S.J., Killen, S.S., Wahl, D.H., Philipp, D.P., Tufts, B.L., 2005. Behaviour of walleye, *Sander vitreus*, and largemouth bass *Micropterus salmoides*, exposed to different wave intensities and boat operating conditions during livewell confinement. Fish. Manag. Ecol. 12, 19–26.

Swenson, W.A., 2002. Demographic changes in a largemouth bass population following closure of the fishery. In: In: Phillipp, D.P., Ridgway, M.S. (Eds.), Black Bass: Ecology, Conservation, and Management. Am. Fish. Soc. Symp., vol. 31. pp. 627–637.

Trippel, N.A., Hargrove, J.S., Leone, E.H., Austin, J.D., Allen, M.S., 2017. Angling-induced impacts on recruitment and contributions to reproduction in Florida bass. Trans. Am. Fish. Soc. 146, 871–887.

van Poorten, B.T., Post, J.R., 2005. Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. North Am. J. Fish. Manag. 25, 329–345.

Waters, D.S., Noble, R.L., Hightower, J.E., 2005. Fishing and natural mortality of adult largemouth bass in a tropical reservoir. Trans. Am. Fish. Soc. 134, 563–571.

Weathers, K.C., Newman, M.J., 1997. Effects of organizational procedures on mortality of largemouth bass during summer tournaments. North Am. J. Fish. Manag. 17, 131–135.

Wege, G.J., Anderson, R.O., 1978. Relative weight (Wr): a new index of condition for largemouth bass. In: In: Novinger, G.D., Dillard, J.G. (Eds.), New Approaches to the Management of Small Impoundments. Am Fish. Soc. N. Central Div. Sp. Pub., vol. 5. pp. 79–91.

Wilde, G.R., Pope, K.L., 2008. Simple model for predicting survival of angler-caught and released largemouth bass. Trans. Am. Fish. Soc. 137, 834–840.

Wilde, G.R., Pope, K.L., Durham, B.W., 2003. Lure-size restrictions in recreational fisheries. Fisheries 28, 18–26.

Wilde, G.R., 1998. Tournament-associated mortality in black bass. Fisheries 23, 12–22.