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ABSTRACT

Largemouth bass *Micropterus salmoides* abundance has increased in many northern lakes over the last decade and this trend may continue based on projected changes in climate. Density-dependent effects on largemouth bass growth and size structure and the potential for bass interactions with other popular sport fish such as walleyes *Sander vitreus* are concerns among anglers and biologists. To reduce largemouth bass abundance, the statewide minimum 14-in total length (TL) limit for bass has been removed from some northern Wisconsin lakes. However, low rates of exploitation may prevent significant reductions in largemouth bass abundance. My objective was to use predictive modeling to determine if largemouth bass abundance, recruitment potential, and size structure in four northern Wisconsin lakes would change in relation to instantaneous fishing mortality rates (*F*) and under different harvest regulations. During 2012 and 2013, I described population demographics and dynamics of largemouth bass populations in Big Arbor Vitae, Big Sissabagama, Little John, and Teal Lakes in northern Wisconsin and used this information to formulate population models for each lake. Models were used to simulate effects of *F* between 0 and 0.9 on predicted abundance of largemouth bass ≥ 8 in TL, relative stock density of largemouth bass ≥ 15 in TL (RSD-15”), and spawning potential ratio (SPR) under the following harvest regulations: 1) current statewide minimum length limit of 14-inches; 2) 14-in maximum length limit; 3) no minimum length limit; 4) 12- to 15-in harvest slot length limit (i.e., fish between 12- and 15-in can be harvested); 5) catch-and-release and 6) 18-in minimum length limit. No minimum length limit had the greatest potential for reducing largemouth bass abundance by ≥ 25%, but relatively high levels of fishing mortality for
Wisconsin bass fisheries ($F \geq 0.2$) were necessary to achieve this reduction. Abundance was reduced $\geq 25\%$ under other harvest regulations, but only at rates of $F \geq 0.3$. Similarly, reducing SPR to $\leq 30\%$ was more likely to occur under a 14-in maximum length limit or no minimum length limit, but only if $F \geq 0.15$. Catch-and-release and an 18-in minimum length limit maximized RSD-15”. However, RSD-15” differed among harvest regulations by $< 10\%$ when $F$ was $\leq 0.10$, which suggests that changing harvest regulations may have little effect on size structure in most Wisconsin largemouth bass fisheries because available data suggests exploitation rates are typically $\leq 10\%$. A 14-in maximum length limit and a 12- to 15-in harvest slot limit provided the most equitable trade-offs between reductions in abundance and maintaining size structure, which is of great interest to fishery managers. My results suggest that altering harvest regulations for largemouth bass in these 4 Wisconsin lakes would not likely change largemouth abundance and size structure if rates of $F$ are $\leq 0.10$. Consequently, if reducing largemouth bass abundance is a primary management objective, targeted removal of bass or angler education or incentive programs may be necessary to achieve levels of $F$ predicted to achieve this objective.
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Table 1.—Parameter estimates used in population models for largemouth bass in four northern Wisconsin lakes. General model parameters include initial abundance ($N_0$) with 95% confidence limits (in parentheses), instantaneous fishing mortality rates ($F$), density-independent ($\alpha$) and density-dependent parameters ($\beta$) and multiplicative process errors ($\epsilon$) for Ricker stock-recruitment relationships. Sex-specific model parameters include estimates of asymptotic total length ($L_\infty$), Brody-Bertalanffy growth coefficients ($K$), and $x$-intercepts ($t_0$) from von Bertalanffy growth models, age at 50% maturity ($A_m$) and shape parameters ($r$) from age-at-maturity relationships and instantaneous natural mortality rates ($M$) estimated from Pauly (1980) models. Age-based parameter estimates for all lakes were based on estimates from sectioned otoliths with exception of Little John Lake, where dorsal spines were used for age estimation.
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INTRODUCTION

Food-web relationships can be complex, and changes in predator abundance or diversity can have substantial effects on population and community dynamics (Polis and Strong 1996). In aquatic ecosystems, introductions of new piscivores can eliminate or reduce abundance of native species (He and Kitchell 1990; Whittier and Kincaid 1999; Findlay et al. 2000; Jackson 2002), alter food web dynamics (Sih et al. 1985; MacRae and Jackson 2001; Baxter et al. 2004; Eby et al. 2006) or negatively affect existing fisheries (McDowall 1968; Reimers 1989; Bacheler et al. 2004). Additionally, increases in abundance of native piscivores can affect the abundance, species diversity, and behavior of prey fish, which in turn may affect lower trophic levels (Carpenter et al. 1985; Drenner and Hambright 2002; Lathrop et al. 2002).

Largemouth bass *Micropterus salmoides* are opportunistic predators that occur in many North American waters. The native range of largemouth bass in North America extends north from northeastern Mexico to southern Quebec and Ontario, and east from the Rocky Mountains to the Mississippi Valley and Great Lakes, through the Gulf of Mexico, and into Florida and the Carolinas (Becker 1983). Through extensive introductions, largemouth bass now exist in all of the contiguous United States as well as British Columbia, Saskatchewan, and much of Mexico (Brown et al. 2009). Additionally, with global temperatures predicted to increase by 1.8–4.0 °C by 2100 (Intergovernmental Panel on Climate Change 2001), warm-water species like largemouth bass are likely to expand their existing range and bass abundance in north-temperate lakes is likely to increase (Shuter and Post 1990; De Stasio et al. 1996; Chu et al. 2005).
Warmer temperatures also could result in faster largemouth bass growth rates, higher first-year survival, and increased recruitment (Shuter and Post 1990; Garvey et al. 2002).

Largemouth bass inhabit a variety of waters including rivers, ponds, lakes, and impoundments, and prefer warm, shallow water with vegetation for cover (Becker 1983; Cooke and Philipp 2009). Male largemouth bass build nests on firm substrate when water temperatures reach 15.6 °C and begin spawning at 16.7–18.3 °C (Becker 1983; Etnier and Starnes 1993). Fecundity typically ranges from 2,000 to 20,000 eggs per female and an average nest contains 5,000 eggs (Becker 1983). After 3–7 days, eggs hatch and the males guard the fry until dispersal, which typically occurs two weeks after hatching (Robbins and MacCrimmon 1974; Becker 1983). Age-0 largemouth bass primarily feed on small crustaceans such as Daphnia spp. and chironomid larvae. As age-0 bass grow larger, they eat aquatic insect larvae, small fish, and larger crustaceans like amphipods and crayfish (Clady 1974; Robbins and MacCrimmon 1974; Cooke and Philipp 2009). Adult largemouth bass feed mainly on fish, crayfish, and other organisms such as frogs, tadpoles, and small mice (Clady 1974; Robbins and MacCrimmon 1974; Becker 1983).

Wisconsin lies along the northern edge of the native range of largemouth bass. Largemouth bass are native to many waters within the state, but they have also been introduced into some waters where they did not previously occur (Becker 1983). Largemouth bass have been documented in 65% of Wisconsin lakes and likely occur in thousands of additional bodies of water (Simonson 2001). A reported 403,000 anglers fished for black bass (i.e., largemouth and smallmouth bass Micropterus dolomieu) in Wisconsin during 2006, which represented more than 4.2 million angler days (U.S.
Department of the Interior 2006). In Wisconsin, the Wisconsin Department of Natural Resources (WDNR) also registered 31,246 black bass caught during tournaments in 2011 (Boehm and Hansen 2011).

Since 1990, mean catch per effort (CPE; catch per mile) of largemouth bass in WDNR angler creel surveys has increased statewide (Figure 1; WDNR, unpublished data) and, more specifically, angler CPE of bass reported in creel surveys has increased in northern Wisconsin (Figure 2). Increases in largemouth bass abundance can result in slower growth (Goedde and Coble 1981; Gabelhouse 1987; Miranda and Dibble 2002), thereby leading to declines in size structure and angling quality (Eder 1984; McHugh 1990; Dean et al. 1991; Dean and Wright 1992).

Currently, statewide harvest regulations for inland waters of Wisconsin allow harvest of largemouth bass from the first Saturday in May to the first Sunday of the following March. The statewide daily bag limit is 5 fish, with a 14-in minimum total length limit (MLL), and special regulations for many individual waters. In a number of other waters vary in the harvest season, and length and bag limits.

The effect of increased largemouth bass abundance on other popular sportfish is also a concern for anglers and fishery managers. Largemouth bass and walleye Sander vitreus may negatively interact in Wisconsin waters (Repp 2012) as increases in largemouth bass density coincide with decreases in walleye density. The possible mechanisms are numerous, including competition for prey, habitat, and other resources. Additionally, largemouth bass reduce survival of walleye stocked into Wisconsin lakes (Fayram et al. 2005). The interactions between largemouth bass and walleye have been an area of major research for the WDNR and is a leading WDNR research need (J.
Hansen, pers. comm.). Recent research has demonstrated that largemouth bass predation of walleye rarely occurred in four northern Wisconsin lakes, but diet overlap between the two species was evident (Kelling 2014). Additionally, largemouth bass and northern pike *Esox lucius* may compete for food resources because their diets can be similar (Paukert and Willis 2003), although one study in Minnesota suggested that largemouth bass are not likely to strongly effect northern pike survival through competition for prey (Soupir et al. 2000). In Alabama, removal of largemouth bass allowed for higher bluegill *Lepomis macrochirus* and crappie *Pomoxis* spp. recruitment (McHugh 1990). In Kansas, bluegill recruitment, longevity, and body condition increased after largemouth bass were removed (Gabelhouse 1987) and age-0 largemouth bass predation on early-spawned age-0 fish was a substantial component of bluegill mortality in Illinois (Santucci and Wahl 2003). Finally, through competition and predation, largemouth bass reduced size structure and abundance of crappies in small Oklahoma impoundments (Boxrucker 1987).

In response to declining walleye abundance, the WDNR removed the statewide 14-in minimum length limit for largemouth bass on 26 lakes in northwest Wisconsin to increase angler harvest of largemouth bass and thereby to reduce bass abundance. In Washburn and Burnett counties, all lakes have no minimum length limit for largemouth bass to allow angler harvest of smaller fish with the intent of increasing bass growth rates. Similarly, harvest regulations for smallmouth bass have been changed on some lakes in Minnesota and Ontario to promote harvest of smaller fish (Isermann et al. 2013). High abundance of largemouth bass can result in slow growth and poor size structure, so protected slot-length limits have been used in other states to alleviate these issues by
allowing for increased harvest of small bass (Eder 1984; Novinger 1984; Neumann et al. 1994; Wilde 1997). However, changes in harvest regulations have not always achieved management objectives (Mraz 1964; Paragamian 1982; Gabelhouse 1987; Martin 1995; Wilde 1997). For example, evaluations of 91 largemouth bass length limits across the USA suggest that minimum length limits generally did not increase largemouth bass abundance, whereas slot-length limits increased size structure (Wilde 1997).

Historically, angler harvest was effective in reducing largemouth bass abundance in many waters (Farabee 1974; Graham 1974; Hickman and Congdon 1974; Rasmussen and Michaelson 1974; Siedensticker 1994), so fishery managers routinely used stricter harvest regulations to increase abundance and size structure of largemouth bass populations (Wilde 1997; Carlson and Isermann 2010). However, changes in angler attitudes regarding harvest of largemouth bass could affect the effectiveness of harvest regulations designed to reduce bass abundance (Allen et al. 2008). Previous studies have demonstrated that voluntary angler release of black bass has increased in North America (Myers et al. 2008; Isermann et al. 2013) and this trend has also been observed in the state of Wisconsin, where, on average, anglers currently harvest less than 5% of the largemouth bass they catch (Gaeta et al. 2013; J. Hansen, WDNR, in press). If anglers voluntarily release most of the largemouth bass they catch, liberalizing harvest regulations may not reduce largemouth bass abundance.

Additionally, biologists do not fully understand the relationship between adult bass abundance and recruitment. Largemouth bass recruitment appears to be largely regulated by abiotic factors (Kramer and Smith 1962; Kohler et al. 1993; Garvey et al. 2002), so abundance of adult fish has little influence on recruitment (Post et al. 1998;
Allen et al. 2011; Siepker and Michaletz 2012). If largemouth bass recruitment in northern Wisconsin lakes is primarily driven by abiotic factors, then increased harvest of bass may not reduce future abundance. Conversely, large-scale removal of smallmouth bass (N = 53,947) from a New York lake resulted in increased abundance of juvenile bass, which suggests an over-compensatory relationship between adult abundance and recruitment requiring substantial removal of adults to reduce recruitment and abundance (Zipkin et al. 2008).

Fishery managers are interested in using harvest regulations to achieve a variety of management objectives for largemouth bass populations in Wisconsin. For some populations, managers want to reduce largemouth bass abundance to improve bass growth and size structure or to reduce potential negative interactions with other popular sportfish. Conversely, in other populations managers may want to maintain or increase bass density to maintain or improve panfish size structure. Lastly, in largemouth bass populations that already provide reasonable numbers of large fish, managers may want to implement regulations that maintain fishery quality in terms of size structure, in some cases while still reducing abundance. The WDNR Bass Species Team will be selecting harvest regulations for largemouth bass that could be used by managers to achieve these and other specified management objectives. However, the response of largemouth bass populations to changes in fishing mortality and harvest regulations has not been well defined for populations in north-temperate lakes.

My objective was to use predictive modeling to determine if largemouth bass abundance, recruitment potential, and size structure would change in relation to fishing mortality under different length-based harvest regulations in four northern Wisconsin
lakes. To achieve my objective, I used sex-specific age-structured largemouth bass population models. I expected to find that the 14-in minimum length limit would not reduce abundance effectively but a no minimum length limit would, and that other harvest regulations (e.g., a harvest slot limit, maximum length limit) may provide trade-offs between reducing abundance and maintaining size structure. My findings would be useful for determining if angling harvest regulations can be used to manipulate largemouth bass abundance and density in Wisconsin.

METHODS

Study Area

Adult largemouth bass were collected from four northern Wisconsin lakes during May–June 2012 and 2013. Lakes were not selected at random, but rather in consultation with WDNR personnel. We selected lakes in which largemouth bass abundance increased recently, based on CPE in electrofishing surveys.

During 2012, we collected largemouth bass from Big Sissabagama and Teal Lakes in northwestern Wisconsin. Big Sissabagama Lake is a meso-eutrophic, 805-acre seepage lake located near the town of Stone Lake in southwestern Sawyer County, Wisconsin (latitude: 45° 47’ 27.24”, longitude: 91° 31’ 4.62”) with 8.2 miles of shoreline and a mean depth of 16 feet. Teal Lake is a eutrophic, 1,024-acre drainage lake located in the Chequamegon National Forest in Sawyer County, Wisconsin (latitude: 46° 5’ 8.40”, longitude: 91° 6’ 15.45”) that has 8.8 miles of shoreline and a mean depth of 15 feet. Fish communities in both lakes included muskellunge *Esox masquinongy*, bluegill,
pumpkinseed *Lepomis gibbosus*, black crappie *Pomoxis nigromaculatus*, yellow perch *Perca flavescens*, largemouth bass, smallmouth bass, northern pike, and walleye.

During 2013, we collected largemouth bass from Big Arbor Vitae and Little John Lakes in northeastern Wisconsin. Big Arbor Vitae Lake is a mesotrophic, 1,070-acre drainage lake located near Minocqua, WI in south-central Vilas County, WI (latitude: 45° 55’48.96”, longitude: 89° 38’59.07”) with 7.8 miles of shoreline and a mean depth of 18 feet. Little John Lake is a 151-acre, mesotrophic spring lake near the University of Wisconsin’s Trout Lake Field Station in Vilas County, WI (latitude: 46° 0' 52.32", longitude: 89° 38' 42.96") with 3.3 miles of shoreline and a maximum depth of 19 feet. Muskellunge, bluegill, pumpkinseed, black crappie, yellow perch, largemouth bass, and walleye are found in Big Arbor Vitae Lake. Muskellunge, bluegill, pumpkinseed, black crappie, yellow perch, largemouth and smallmouth bass, northern pike, and walleye are found in Little John Lake.

**Sampling**

During May and June of each year, largemouth bass were collected on a minimum of three sampling dates using AC boat electroshocking conducted at night. On each sampling date, largemouth bass were collected at five or more randomly-selected, 20-min shoreline transects. All largemouth bass collected were measured to the nearest mm (TL) and weighed to the nearest g and, when possible, sex was determined by extrusion of gametes. On Big Sissabagama, Teal, and Big Arbor Vitae lakes, at least 5 male and 5 female bass were sacrificed within each 1-in TL interval for otolith removal and fecundity estimation, and at least 10 fish were sacrificed for smaller length intervals,
typically ≤ 8-in, where sex could not be easily determined in the field. Sacrificed fish were individually frozen for further analysis. Because Little John Lake is relatively small (151 acres) and largemouth bass abundance was expected to be low (< 500 fish; S. Gilbert, WDNR, personal communication), sacrificing up to 10 bass per inch group for otoliths could negatively affect the population of bass. Using the same length-based sampling strata, I removed the 3rd dorsal spines (Logsdon 2007; Morehouse et al. 2013) as a nonlethal alternative to estimate age of bass from Little John Lake. All largemouth bass that were released were marked with a partial clip of the left pectoral or ventral fin for estimating abundance by mark-recapture and all bass captured in subsequent surveys were examined for presence of fin clips. We assumed that partial fin clips generally did not affect fish survival and were discernible throughout our 4-6 week sampling period (Wydoski and Emery 1983).

For largemouth bass removed from each lake, gonads were examined to determine sex and maturity, and ovaries and sagittal otoliths were removed. Ovaries were weighed to the nearest 0.01 g and preserved in 10% buffered formalin. Fecundity was estimated for each female fish using a gravimetric approach, where eggs were enumerated in 0.1-g subsamples removed from randomly-selected locations throughout the ovary with forceps (Laarman and Schneider 1985). The number of eggs per g was calculated for each subsample and the mean number of eggs per g for all subsamples was multiplied by total ovary weight to estimate fecundity of each fish. To determine the minimum number of 0.1-g subsamples needed to estimate fecundity for an individual female, I counted 30 subsamples from ovaries of four different fish that represented the entire TL range of female fish in the sample. For each individual number of subsamples
(i.e., 1–30 subsamples), fecundity was estimated by multiplying the mean number of eggs per g of ovary (i.e., a running average) by total ovary weight. For each of the four females, I determined the number of subsamples that were required to ensure that my fecundity estimate was within the 95% confidence interval of the fecundity estimate that would have been obtained by counting all 30 subsamples. I averaged this value across four fish and determined that five subsamples of 0.1 g should be counted per female.

Thin-sectioned sagittal otoliths were used to estimate ages of largemouth bass from Big Sissabagama, Teal, and Big Arbor Vitae Lakes (Buckmeier 2003). Otoliths from each largemouth bass were embedded in epoxy resin and thin sectioned (1.2 mm) along the transverse plane through the nucleus using a low speed saw (Buehler® Isomet® 1000 Precision Saw with a 0.4 mm diamond wafering blade) for a section width of 0.8 mm. Sectioned otoliths were mounted to glass microscope slides with cyanoacrylic cement and allowed to dry for 24 h. Otolith sections were polished with wetted 1,000 grit sandpaper and immersion oil was applied to improve image clarity. All sectioned otoliths were read independently by two readers using transmitted light and a Nikon® Eclipse SMZ1500 dissecting microscope. When < 2 annuli were visible on a sectioned otolith, the whole otolith was also examined. If the two readers disagreed on age, the otolith section was interpreted by a third reader to obtain a consensus age for the fish (i.e., at least 2 of 3 readers agreed on an age). If a consensus age could not be obtained, the structure was omitted from analysis.

For estimating age of largemouth bass from Little John Lake, I removed remaining flesh from the base of each dorsal spine and polished the base with wetted 1,000-grit sandpaper. The distal end of each spine was inserted into a dish of plumber’s
putty so that the polished base was facing up. A fiber optic light (0.032” aperture) was
moved along the edge of the polished base to illuminate annuli. Immersion oil was
applied to improve image clarity. All dorsal spines were examined by two readers. If the
two readers disagreed on age, the dorsal spine was interpreted by a third reader to obtain
a consensus age for the fish (i.e., at least 2 of 3 readers agreed on an age). If a consensus age could not be obtained, the structure was omitted from analysis.

**Population metrics**

All modeling and calculations were completed in Microsoft Excel® 2010
(Microsoft Corporation, Redmond, Washington) unless otherwise noted. I used the
Schnabel estimator (Schnabel 1938) to estimate abundance of largemouth bass ≥ 8-in TL
in Big Sissabagama, Big Arbor Vitae, and Little John Lakes by treating each sampling
date t as a mark-recapture event:

\[
\hat{N} = \frac{\sum_{t=1}^{i} (C_tM_t)}{\sum_{t=1}^{i} R_t}
\]

where \(C_t\) = number of individuals caught at time \(t\), \(M_t\) = total number of marked
individuals in the population at time \(t\), and \(R_t\) = number of marked individuals recaptured
at time \(t\). Exact binomial 95% confidence limits were calculated for each population estimate using the formulas provided by Zar (1996) where the lower 95% confidence
limit for R/C was calculated as:

\[
L_1 = \frac{R}{R + (C - R + 1)F_{\alpha(2),V_1,V_2}}
\]
where:

\[ V1 = 2(C - R + 1), \]

and:

\[ V2 = 2R. \]

The upper confidence limit for R/C was calculated as:

\[ L2 = \frac{(R+1)F_{\alpha(2),V1'V2'}}{C-R+ (R+1)F_{\alpha(2),V1'V2'}}, \]

where:

\[ V1' = 2(R + 1) = V2 + 2, \]

and:

\[ V2' = 2(C - R) = V1 - 2. \]

I did not recapture any largemouth bass in Teal Lake during our May-June sampling period, so to obtain an estimate of adult bass abundance, I first converted mean electrofishing CPE (catch per hour) during May and June to catch per km using a relationship developed from WDNR electrofishing surveys (Repp 2012):

\[ \text{Bass per km} = 0.325 \times (\text{bass per hour}) + 0.47. \]

I converted mean catch of largemouth bass per km to mean catch per mile and used the following relationship to estimate bass density for Teal Lake:

\[ \frac{N}{A} = \left( \frac{(C/f)}{\alpha} \right)^{1/\beta}, \]

where \( C/f \) = bass/mile, \( \alpha \) = catchability at low population density, \( N/A \) = bass/acre, and \( \beta \) = the degree of curvature between \( C/f \) and \( N/A \). I used bias-corrected estimates and 95%
confidence intervals of $\alpha$ ($\alpha = 3.04$, 95% CI: 2.52-3.67) and $\beta$ ($\beta = 0.88$, 95% CI: 0.69-1.06) provided by Schoenebeck and Hansen (2005) for spring largemouth bass electrofishing in Wisconsin lakes to estimate N/A and associated 95% confidence intervals. I then multiplied values of N/A by lake surface area to obtain adult largemouth abundance and 95% confidence intervals for Teal Lake.

To describe size structure of adult bass in each lake, I allocated the estimated number of bass $\geq$ 8-in TL to 1-in TL intervals based on the length frequency distribution of fish captured during electrofishing. Sex-specific abundance of bass within each 1-in TL interval was calculated by multiplying the number of fish allocated to the TL interval by the proportion of male and female fish within the interval during electrofishing. I constructed sex-specific age-length keys to estimate sex-specific age frequency distributions that were used to initiate model simulations (Isermann and Knight 2005).

Because length-stratified subsampling was used to obtain fish for age estimation, I calculated mean lengths at age using a weighted-means approach (Bettoli and Miranda 2001). Growth trajectories of male and female bass in each lake were estimated using sex-specific von Bertalanffy models fit to mean lengths at age by using nonlinear least-squares regression:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) + \varepsilon_i$$

where $L_t$ = mean length at age of capture $t$, $L_\infty$ = average asymptotic maximum length, $K$ = instantaneous rate at which $L_t$ approaches $L_\infty$, and $t_0$ is the x-intercept, and $\varepsilon_i$ is additive error.

I estimated sex-specific instantaneous natural mortality ($M$) for each population using $L_\infty$ and $K$ from the von Bertalanffy growth model (Pauly 1980):
\[ \log_{10} M = -0.0066 - 0.279 \times \log_{10}(L_\infty) + 0.6543 \times \log_{10}(K) + 0.4634 \times \log_{10}(T), \]

where \( T = \) mean annual air temperature (°C) for the region. Mean annual air temperature corresponds to mean annual water temperature (Pauly 1980; Shuter et al. 1983) and were used because mean annual water temperature was not available for each lake. Mean annual air temperature data was acquired from the National Climatic Data Center (NOAA) for the last 30 years (1981–2010) to estimate average mean annual air temperature over the 30-year interval for Big Arbor Vitae and Little John Lakes (41.03 °C) and Big Sissabagama and Teal Lakes (41.83 °C).

Sex-specific maturity-at-age relationships were estimated for each population using the logistic model:

\[ M_i = \frac{1}{1 + e^{-r(i + A_m)}}, \]

where \( M_i \) is the expected proportion of fish mature at age \( i \), \( r \) describes the degree of curvature in maturity-at-age and \( A_m \) is the age at 50% maturity. This relationship was fit by adjusting parameters \( r \) and \( A_m \) to minimize RSS. Largemouth bass ≥ 10 years of age were considered as a single group for this analysis because of low sample sizes and the fact that all fish at these ages were mature.

Fecundity-age relationships were described for each population as:

\[ \varphi = \alpha (age)^\beta, \]

where \( \varphi = \) number of eggs, \( age = \) age of female largemouth bass in years and \( \alpha \) and \( \beta \) represent the parameters of the relationship between fecundity and age for each bass population. I used residual diagnostics to determine that a power function was more appropriate (i.e., lower RSS) for describing fecundity-age relationships than a linear model.
Model Simulations

An age-structured model was used to simulate effects of fishing mortality and different length-based harvest regulations on future largemouth bass abundance, size structure, and recruitment potential for each lake (Figure 3). Simulations were run over 200-year intervals. The initial 50 years of each simulation were used for the “burn-in” period of model calibration; results from the final 150 years were used for evaluation purposes. Males and females represented separate sub-models for each lake because of differences in growth and maturity between sexes, and to estimate changes in recruitment potential. Maximum age for each sex represented the maximum ages observed for each population.

I simulated effects of alternative length-based harvest regulations being considered by WDNR for largemouth bass management: 1) the current 14-in minimum length limit; 2) a 14-in maximum length limit; 3) no length limit; 4) a 12- to 15-in harvest slot length limit (i.e., fish between 12- and 15-in can be harvested); 5) catch-and-release; and 6) an 18-in minimum length limit. The first five regulations were simulated on all lakes. Because length-frequency distributions used to initiate models were based on electrofishing samples, predicted effects of an 18-in minimum length limit was only assessed for Little John Lake because this was the only lake where largemouth bass ≥ 18-in were encountered. These regulations were selected by the WDNR Bass Species Team as regulations of interest with regards to updating the suite of regulations (i.e., regulations “toolbox”) that could be used by biologists to manage largemouth bass populations within the state.
I simulated a range of instantaneous fishing mortality rates ($F$): 0.0, 0.05, 0.10, 0.15, 0.20, 0.30, 0.40, 0.50, 0.60, and 0.9. While achieving rates of $F \geq 0.20$ may be unrealistic for largemouth bass fisheries because of angler attitudes regarding harvest, I simulated a wide range of $F$ to determine the level of harvest needed to reduce future bass abundance in the study lakes. Furthermore, while I did not specifically simulate potential increases in daily bag limits for largemouth bass, the range of $F$ likely encompassed any changes in $F$ that would occur if bag limits were increased. Each model simulation was initiated using sex-specific age frequency distributions for each lake. For each sex, the number ($N$) of age $i$ fish in year $j$ that survived to age $i+1$ was calculated as:

$$N_{(i+1)(j+1)} = (N_{ij})e^{-([F\cdot p_i] + M)},$$

where $p_i$ represents the proportion of age $i$ fish that were vulnerable to harvest under a specific harvest regulation. Age-specific vulnerability to harvest ($p_i$) was based on age-specific TL frequency distributions for each sex. For ages where no fish could be legally harvested under a specific harvest regulation, $p_i = 0$ and only $M$ operated to remove fish. For ages where all fish were of TLs that could be legally harvested, $p_i = 1$ (i.e., fully vulnerable to harvest) and both fishing and natural mortality would operate to remove fish. For ages where some, but not all fish were of TLs that could be legally harvested, $p_i$ was equal to the proportion of fish that were vulnerable to harvest based on TL. For example, if a 14-in minimum length limit was in place, and 10% of the age-5 female largemouth bass were $\geq$ 14-in TL, then $p_i = 0.10$. For length limits where anglers could harvest largemouth bass $\leq$ 14-in TL, I assumed that bass were vulnerable to harvest at 12-in TL. Although angler harvest has not been estimated for bass $\leq$ 14-in TL because of the statewide 14-in MLL, I chose to begin vulnerability to harvest at 12-in TL because it
corresponds to the largemouth bass proportional stock density (PSD) “quality” length and anglers often release most bass ≤ 12-in TL even when harvest is allowed (Gabelhouse 1984; Wilde 1997; Summers 1990; Martin 1995). Additionally, few largemouth bass ≤ 12-in were harvested from several Minnesota lakes where harvest of largemouth bass ≤ 12-in was allowed (Maloney et al. 1962; MNDNR 1996; Pelham 2006).

The number of age-1 recruits for year \( j+1 \) \( (R_{j+1}) \) resulting from spawner abundance in year \( j \) \( (S_j) \) was simulated using a Ricker stock-recruitment model (Ricker 1975):

\[
R_{j+1} = (\alpha S_j e^{-\beta S_j e^\epsilon}),
\]

where \( S_j \) is the number of sexually-mature largemouth bass of both sexes in year \( j \), \( \alpha \) was the density-independent parameter (i.e., rate of recruitment \( R/S \) before density-dependence begins), \( \beta \) was the density-dependent parameter (i.e., the instantaneous rate of decline in \( R/S \) as \( S \) increases), and \( e^\epsilon \) was the lognormal error term (Allen et al. 2011).

I calculated sex-specific values of spawner abundance for each year \( S_j \) as:

\[
S_j = \sum_{i=1}^{n} N_{ij} \times M_i,
\]

where \( M_i \) is the observed proportion of mature bass at age \( i \). I summed values of \( S_j \) for both sexes to obtain values of \( S_j \) that were used in the Ricker stock-recruitment model. The Ricker model reflects an overcompensatory relationship, where interaction(s) between adults and young result in low recruitment at high spawner abundance. I chose to use the Ricker stock-recruitment model because: 1) largemouth bass are known to be cannibalistic (Clady 1974; Johnson and Post 1996; Hodgson et al. 2006); 2) consistently low largemouth bass recruitment at relatively high adult and juvenile abundance suggests
cannibalism as a possible mechanism regulating recruitment (Post et al. 1998) and 3) an overcompensatory stock-recruit response was evident in a smallmouth bass population in New York (Zipkin et al. 2008).

No previous study has explicitly reported parameters ($\alpha$ and $\beta$) of a Ricker stock-recruitment relationship for a largemouth bass population and the data necessary to estimate these parameters were not available for Wisconsin bass populations. Consequently, I obtained parameters for the Ricker stock-recruitment relationship by estimating the peak of the stock-recruitment curve ($X = 1/\beta$; $Y = a/\beta e$) under the assumption that the study populations were lightly exploited and near carrying capacity (Ricker 1975; Hansen et al. 2010). For each population, the number of spawning largemouth bass ($X$) predicted to produce the maximum number of recruits ($Y$) was estimated from sex-specific abundance resulting from mark-recapture surveys and maturity-at-age relationships. The expected number of age-1 recruits ($Y = a/\beta e$) resulting from $X$ was estimated using back-transformed intercepts of catch curves that were fit using abundance at age information for each population (Ricker 1975; Hansen et al. 2010). Catch curves were constructed by regressing log$_e$ abundance at age, beginning at ages where $\geq 50\%$ of largemouth bass were $\geq 8$-in, the length at which bass were considered fully vulnerable to electrofishing. Consequently, the parameters $\alpha$ and $\beta$ were estimated as:

$$\beta = \frac{1}{X},$$

and:

$$\alpha = \frac{Y}{X \times e}.$$
I estimated stock-recruitment parameters for Big Arbor Vitae, Big Sissabagama, and Teal largemouth bass populations using this approach. The estimate of $\alpha$ for Little John Lake provided nonsensical estimates of adult abundance (i.e., estimates far outside the 95% confidence intervals for the population estimates from sampling). As a result, I used the average value of $\alpha$ estimated from the other 3 lakes for Little John Lake.

To simulate recruitment variation resulting from factors other than adult abundance (i.e., process error), I used coefficient of variation (CV = SD/mean) from age-0 largemouth bass seine CPE (catch per seine haul; CV = 0.59) observed over a three-year period on Minocqua and Squaw lakes in Oneida County, Wisconsin (C. Kelling, UWSP, unpublished data). Variation in age-0 largemouth bass CPE in seine hauls was similar to the mean CV in age-0 CPE reported for 13 largemouth bass populations in the southeastern United States (0.66; Allen and Pine 2000). Variation in largemouth bass recruitment (i.e., number of age-1 recruits per spawning bass) was incorporated into the lognormal error term of the stock-recruit relationship using the Excel® function:

\[
\text{LOGINV}(p, \mu, \sigma)
\]

where $p$ was randomly selected between 0.0 and 1.0 with the Excel® function RAND(), $\mu$ = 0, and $\sigma$ = 0.59 (Haddon 2001; Allen et al. 2012).

Each 150-year harvest regulation scenario was repeated 50 times and mean adult abundance for each 150-year period was averaged across all 50 simulations. To summarize, for each of the six harvest regulation scenarios I ran simulations at 10 different levels of $F$ and each of these simulations was repeated 50 times. I described changes in adult ($\geq$ 8-in) largemouth bass abundance expected under different harvest scenarios as:
\[
\text{% reduction} = 1 - \frac{A_{kF}}{A_{k0}},
\]

where \(A_{k0}\) is mean adult abundance of bass observed under harvest regulation \(k\) when \(F = 0.00\) and \(A_{kF}\) is the mean abundance of bass under regulation \(k\) at a selected level of \(F\). I was specifically interested in harvest scenarios that resulted in reductions in abundance of \(\geq 25\%\) and \(\geq 50\%\) because I considered these as reduction goals likely to be acceptable to fishery managers.

Relative stock density of largemouth bass \(\geq 15\)-in TL (RSD-15”) values were used to describe trends in size structure. When each 150-year harvest regulation scenario was repeated 50 times, the RSD values were averaged over the 50 simulations. RSD-15” was calculated as:

\[
\frac{\text{number of bass} \geq 15 \text{ in TL}}{\text{number of bass} \geq 8 \text{ in TL}}.
\]

I chose RSD-15” because it is often used by managers to describe size structure of largemouth bass populations (Eder 1984; Wilde 1997). I was specifically interested in harvest scenarios that resulted in improvements in RSD-15” \(\geq 10\%\) because I considered this the minimum level of improvement that might be acceptable to goal by fishery managers.

As an additional, more traditional, method for describing the effects of \(F\) on recruitment potential of bass in each lake under different harvest regulations, we used static spawning potential ratio (SPR):

\[
\text{SPR} = \left( \frac{\text{EPR}_{\text{exploited}}}{\text{EPR}_{\text{max}}} \right) \times 100,
\]

where \(\text{EPR}_{\text{max}}\) is the expected lifetime fecundity of an age-1 bass recruit (i.e., eggs per recruit) in the absence of \(F\) and \(\text{EPR}_{\text{exploited}}\) is the expected lifetime fecundity of an age-1
recruit under a specific harvest regulation at a specified level of $F > 0$. Static SPR assumes that growth, survival, maturation, and fecundity are not affected by density. Estimates of $EPR$ were calculated using the formula provided in Boreman (1997):

$$EPR = \sum_{i=1}^{n} M_{Fi} \varphi_i \prod_{j=0}^{i-1} S_{ij}$$

where $n =$ number of ages in the unexploited population, $M_{Fi} =$ percentage of age $i$ females spawning each year, $\varphi_i =$ mean fecundity of age $i$ females, and $S_{ij} =$ annual survival rate of age $i$ females during period $j$. Essentially, $EPR$ represents a sum of the products of fecundity at age and age-specific survival rates. Mace and Sissenwine (1993) suggested that a range of SPRs from 20% to 30% could be used to prevent recruitment overfishing for marine species that are relatively resilient to fishing mortality (Mace and Sissenwine 1993). However, given the resiliency of largemouth bass, I used a threshold SPR of 10% to identify harvest scenarios that could result in recruitment overfishing of largemouth bass in my four study lakes. Spawning potential ratios were not calculated for Little John Lake due to the small number of largemouth bass sacrificed.

**RESULTS**

*Abundance*

A variety of harvest regulations and levels of $F$ were necessary to achieve reductions in largemouth bass abundance $\geq 25\%$. No minimum length limit was predicted to reduce adult abundance by $\geq 25\%$ at $F = 0.2$ in Big Sissabagama and Little John lakes, and at $F = 0.3$ in Big Arbor Vitae Lake, whereas predicted reductions in abundance of largemouth bass were always $< 25\%$ under all length limits in Teal Lake.
In Big Arbor Vitae Lake, a 12- to 15-in harvest slot length limit also reduced adult abundance ≥ 25% at $F = 0.2$ (Figure 9). A 12-to 15-in harvest slot length limit and a 14-in maximum length limit also reduced adult largemouth abundance ≥ 25% at $F = 0.30$ in Big Sissabagama and Little John Lakes, but this regulation was not predicted to reduce abundance by ≥ 25% in Teal Lake.

Abundance was reduced ≥ 50% in Big Sissabagama Lake under no minimum length limit, a 12- to 15-in harvest slot length limit, and a 14-in maximum length limit, but only when $F \geq 0.5$, which was also true for no minimum length limit and a 12- to 15-in harvest slot length limit for Big Arbor Vitae Lake (Figure 9). For Little John Lake, no minimum length limit reduced adult largemouth bass abundance by ≥ 50% when $F$ was ≥ 0.5, but a 12- to 15-in harvest slot length limit and a 14-in maximum length limit were not likely to reduce abundance ≥ 50%.

Size structure

Differences in RSD-15” among harvest regulations for all lakes were < 10% when $F$ was ≤ 0.10 (Figure 10). Catch and release only and an 18-in minimum length limit maximized RSD-15” in all lakes. Specifically, RSD-15” under these two regulations was at least 20-30% higher at $F \geq 0.2$ when compared to other regulations, except in Teal Lake (Figure 10). With the exception of Teal Lake, no minimum length minimized RSD-15” compared to all other regulations. Under no minimum length limit, RSD-15” was 20-25% lower than all other regulations when $F \geq 0.2$ (Figure 10).

For all lakes, a 14-in maximum length limit, 14-in minimum length limit, and 12-to 15-in harvest slot limit provided similar values of RSD-15” that were between RSD-
15” observed under catch-and-release only and an 18-in minimum length and RSD-15” observed under no minimum length limit (Figure 10). Of these three intermediate regulations, RSD-15” was predicted to be slightly higher under a 14-in maximum length limit for 2 of the 4 lakes (Big Sissabagama and Big Arbor Vitae Lakes; Figure 10). On Little John Lake, RSD-15” values were highest (≥ 10%) among these three intermediate regulations under a 14-in minimum length limit, but only when $F \geq 0.4$ (Figure 10). This intermediate group of regulations provided similar values of RSD-15” for largemouth bass in Teal Lake (Figure 10).

**Recruitment potential**

As $F$ increased, SPR declined similarly under all harvest regulations, except for a 18-in minimum length limit, under which SPR remained constant (Figure 12). In general, SPR reached 10% with the lowest $F$ (i.e., $F = 0.30$) under a 14-in maximum length limit, followed by no minimum length limit and a 14-in minimum length limit. Spawning potential ratios ≤ 10% occurred in Big Sissabagama Lake under no minimum length limit at slightly lower $F$ than under a 14-in maximum length limit (Figure 12), but all regulations produced very similar results. Spawning potential ratio was reduced to 10% on Big Sissabagama and Teal Lakes under a 14-in maximum length limit when $F = 0.30$ (Figure 12). Besides the 18-in minimum length limit, SPR remained highest under the 14-in minimum length limit and SPR values were ≤ 10% when $F \geq 0.5$ on Big Arbor Vitae and Big Sissabagama Lakes (Figure 12). Spawning potential ratio did not reach 30% in Teal Lake at any level of $F$ (Figure 12).
Discussion

In 3 of 4 study lakes, my model predictions indicated angler harvest could reduce abundance of adult largemouth bass by $\geq 25\%$ when $F \geq 0.20$, but reductions in adult bass abundance of $\geq 50\%$ would require rates of $F$ that are probably unrealistic for these fisheries. My findings are consistent with several previous studies reporting that angler harvest can reduce largemouth bass abundance (Graham 1974; Hickman and Congdon 1974; Rasmussen and Michaelson 1974). A limited set of data (J. Hansen, WDNR, unpublished data) suggests $F$ due to angler harvest alone (i.e., no catch-and-release mortality included) is $< 0.10$ for largemouth bass fisheries in Wisconsin, probably because anglers in the upper Midwest release nearly all largemouth bass they catch (Gaeta et al. 2013; Isermann et al. 2013). In light of my estimates of $M$ (0.07-0.19; Table 1), annual exploitation rates ($u$) of largemouth bass would need to be $\geq 16\%$ to reach values of $F = 0.20$, yet $u$ is probably $< 5\%$ for most bass fisheries in northern Wisconsin (J. Hansen, WDNR, unpublished data). Consequently, substantial increases in angler harvest or targeted removal would be necessary to reduce largemouth bass abundance $\geq 25\%$. Increasing angler harvest to this level would likely require incentives or angler education programs. No minimum length limit was predicted to reduce abundance $\geq 25\%$ at the lowest level of $F$, but was also predicted to provide low RSD-15” in all lakes. A 12- to 15-in harvest slot length limit or a 14-in maximum length limit might also result in $\geq 25\%$ reductions in adult abundance at similar or slightly higher $F$ than no minimum length limit, while providing higher size structure.
Regulations functioned similarly and produced similar results due to the vulnerability to harvest beginning at 12-in TL. Specifically, Teal Lake did not exhibit substantial differences among harvest regulations for most response metrics (i.e., abundance and RSD-15”). For example, reductions in abundance of ≥ 25% and differences in RSD-15” ≥ 10% were not observed with catch-and-release only and a 14-in minimum length limit for Teal Lake. This lack of response occurred because relatively few adult largemouth bass ≥ 12-in TL were observed in Teal Lake. Therefore, most of the bass were not vulnerable to harvest under any regulation because vulnerability to harvest was assumed to begin at 12-in TL.

Using 12-in TL to initiate harvest vulnerability also meant that a 14-in maximum length limit allowed for harvest of largemouth bass 12- to 14-in TL, which represents only a 1-in difference in the range of harvestable TLs when compared to a 12- to 15-in harvest slot length limit. Hence, these two regulations provided similar trends in abundance for almost all lakes (Figure 9) with the exception of Little John Lake, where largemouth bass ≥ 15-in TL were relatively common and removal of these larger bass had a more noticeable effect on abundance (Figure 9). My modeling results demonstrate that the characteristics of individual largemouth bass populations may result in harvest regulations that function almost identically and therefore would be redundant within a regulations “toolbox” provided to fishery managers. Initiating harvest at smaller TLs (e.g., ≤ 11-in TL) would allow for a higher proportion of largemouth bass to be vulnerable to harvest (Figure 6) and could result in a more noticeable changes in abundance and size structure and greater differences in these metrics among regulations.
Differences in population characteristics such as age at maturity and the degree of density-dependence ($\beta$) in a stock-recruitment relationship may contribute to the differences I observed in the predicted responses of largemouth bass populations to harvest regulations. Although I did not incorporate a direct density-dependent relationship into my models, differences in both of these metrics are typically linked to density. However, a clear relationship between these population characteristics and responses to the harvest regulations was not entirely apparent in my study. I expected that Big Sissabagama and Big Arbor Vitae Lakes, which had the lowest $\beta$ values of the four lakes, would be most resilient to harvest. The largemouth bass population in Big Sissabagama Lake exhibited similar trends in abundance reductions as Little John Lake, which had the highest $\beta$ value of any lake, and Big Arbor Vitae required less $F$ than Teal Lake to reduce abundance (Table 1; Figure 9). Age at maturity would be expected to decrease as density increases and the largemouth bass population becomes more resilient to harvest, but the population with the lowest observed age at maturity (Little John Lake) had reductions in abundance that were similar to the population with the highest age at maturity (Big Sissabagama Lake; Table 1; Figure 9). Including additional lakes with greater differences in $\beta$ values and age at maturity may provide more insight into the effects of density-dependence on largemouth bass population responses to harvest regulations.

Differences in RSD-15” $\geq$ 10% were only observed among harvest regulations when $F$ was $\geq$ 0.10. Therefore, changes in largemouth bass harvest regulations will probably not affect size structure in most northern Wisconsin lakes, if we assume that $F$ for these fisheries is usually $< 0.10$. If $F$ exceeds 0.10, the 12- to 15-in harvest slot limit
may reduce abundance, while reducing size structure less than no minimum length limit (Figures 9 and 10). Similarly, Wilde’s (1997) meta-analysis of length-based harvest regulations for largemouth bass indicated that implementing slot length limits increased size structure, but did not increase angler catch rates. Furthermore, size structure of other largemouth bass populations increased in response to harvest slot length limits (Dean and Wright 1992; Neumann et al. 1994), although exploitation rates were higher (21-48%) in these fisheries than northern Wisconsin largemouth bass fisheries.

Generally, a 14-in minimum length limit (i.e., the statewide regulation) was not effective for reducing largemouth bass abundance and provided intermediate values of RSD-15” when compared to other harvest regulations (Figures 9 and 10). Similarly, implementation of a 14-in minimum length limit resulted in increased abundance and increased size structure of largemouth bass in Texas reservoirs (Terre and Zerr 1992). Minimum length limits included in a meta-analysis of several lakes were generally ineffective at accomplishing management goals such as increasing abundance and size structure, although angler catch rates usually increased (Wilde 1997).

Use of dorsal spines for age estimation on Little John Lake likely resulted in some underestimation of largemouth bass age compared to otoliths (Devries and Frie 1996; Isermann et al. 2010), which led to an overestimation of growth and mortality rates and the catch-curve intercept used to derive stock-recruitment parameters. If dorsal spines are to be used to estimate the age of largemouth bass in the future, additional studies to determine the accuracy and precision of using this structure would be prudent.
I did not account for potential density-dependent changes in largemouth bass growth. Largemouth bass growth declines in response to high abundance (Goedde and Coble 1981; Gabelhouse 1987; Miranda and Dibble 2002), thereby reducing size structure and angling quality (Eder 1984; McHugh 1990; Dean et al. 1991; Dean and Wright 1992). While I can assume that reductions in density predicted under some harvest regulations and rates of $F$ could result in increased largemouth bass growth, I did not know the magnitude of reduction in density needed to elicit a growth response, if increases in growth are linearly related to density, or whether these responses occur immediately or the response transpires over several years. If reduced density results in higher largemouth bass growth rates, then some harvest regulations could provide greater improvements in size structure than predicted in my model simulations, while other regulations could maintain or increase bass density, resulting in slow growth and low size structure.

I did not explicitly address the potential effects of catch-and-release mortality in my modeling scenarios. Given the high rate of catch and release in many largemouth bass fisheries (Gaeta 2013; Isermann et al. 2013), mortality associated with catch and release of fish has the potential to significantly affect management decisions, if release mortality is sufficiently high (Kerns et al. 2012). Catch-and-release mortality is rarely estimated for largemouth bass (Kerns et al. 2012), but previous estimates ranged 3-38% mortality (Muoneke and Childress 1994). Incorporating this source of mortality in my modeling simulations would have resulted in greater reductions in abundance and recruitment potential at any level of $F$. Furthermore, because I simulated a wide range of $F$, my modeling results allow for ad hoc assessment of how this additional source of
fishing-related mortality (i.e., $F +$ catch- and-release mortality) might affect abundance, size structure, and recruitment potential of largemouth bass in these 4 lakes.

Estimating stock-recruitment parameters for many fish species can be difficult because long-term data on spawning stock size and recruits are not collected for many populations (Allen et al. 2011) and these data are not available for any largemouth bass population in Wisconsin. Previous studies have examined trends in centrarchid recruitment dynamics by using different indices of relative abundance, such as CPE of adults or age-0 fish, to describe stock-recruitment relationships when estimates of spawner and recruit abundance are not available (Orth 1979; Post et al. 1998; Bunnell 2006; Allen et al. 2011; Siepker and Michaletz 2013). I could not use stock-recruitment parameter estimates from other studies because of differences in data collection or because parameters of stock-recruitment models were not reported. Therefore, I used less conventional and potentially more error prone methods to estimate largemouth bass stock-recruitment relationships. Specifically, $R^2$ values associated with catch curves used to estimate peak recruitment were low ($< 0.5$), representing a potential source of error. However, I believed it was important to incorporate an overcompensatory relationship in my models based on previous evidence of black bass exhibiting this response (Zipkin 2008).

The level of $F$ needed to reduce SPR to $\leq 10\%$ and potentially result in largemouth bass recruitment overfishing varied among lakes, but in general these values of $F$ were higher than can be expected for Wisconsin fisheries. Previously, concern over reductions in largemouth bass SPR has been limited mainly to fishing bass on their nests and the potential need for fishery closures during spawning (Ridgway and Shuter 1997;
Gwinn and Allen 2010), and these studies offered evidence that fishing mortality could be used to achieve recruitment overfishing in some bass fisheries. However, my results reinforce that largemouth bass are more resilient to overfishing than other species like sturgeon (Quist et al. 2002) and that levels of $F$ needed to induce reductions in largemouth bass recruitment may be difficult to achieve given current angler attitudes toward harvest.

**Management Recommendations**

My results provide fishery managers with a framework for assessing the effects of different harvest regulations on largemouth bass populations in my study lakes. If reducing largemouth bass abundance is the primary management objective for a population, my results suggest that no minimum length limit would be the best regulation option, but reducing abundance by $\geq 25\%$ will likely be difficult if $F$ cannot be increased to $\geq 0.2$. Similar levels of fishing mortality would also be needed to facilitate reductions in SPR of $\geq 30\%$. Abundance of largemouth bass could be reduced at lower rates of $F$ if anglers consistently harvested largemouth bass < 12-in TL. Angler education could be used to promote increased harvest of more small bass to increase largemouth bass harvest, but my modeling suggests that these programs would need to result in substantial increases in $F$ to achieve meaningful reductions in abundance.

If increasing population size structure is the primary management objective, fishery managers should consider harvest regulations that allow for harvest of smaller bass, while protecting larger bass. A 14-in maximum length limit and 12- to 15-in harvest slot limit would achieve this objective for most of the study lakes, although at
levels of $F \leq 0.10$, all regulations caused similar RSD-15”. If density-dependent growth is not a concern (i.e., reductions in abundance are not needed), largemouth bass size structure could be maximized by eliminating harvest. However, many lakes in northern Wisconsin may not have the potential to produce sufficient numbers of largemouth bass $\geq 15$-in TL to warrant trophy management, so a 14-in minimum length limit may be sufficient to maximize size structure if density-dependent growth is not a concern.

I recommend that fishery managers use a categorical approach to applying harvest regulations to largemouth bass populations based on management objectives. These management objectives must be realistic in relation to variation in population dynamics of largemouth bass among lakes, including growth and fishing mortality rates. This approach would require additional sampling to acquire information beyond CPE and size structure for more largemouth bass populations within Wisconsin. This might include long-term studies, more intensive sampling (i.e., data sets of length, weight, age, maturity, etc.), and angler motivation. Long-term studies aimed at understanding the extent of density-dependent growth that occurs within Wisconsin largemouth bass populations is important to effective management, because a regulation to improve size structure may not achieve its objective if growth declines as a density increases. However, understanding density-dependent growth would require relatively frequent sampling and collection of age information for at least some individual largemouth bass populations, which would represent a substantial change to current survey protocols. Otoliths, rather than scales, should be used for age estimation in future evaluations of largemouth bass. Understanding largemouth bass vulnerability to harvest when bass < 14-in TL can be legally harvested is important for predicting the effects of harvest.
regulations. If anglers harvest largemouth bass < 12-in TL, then implementing harvest regulations that allow harvest of these fish may be more successful in reducing abundance than predicted from my models. Because some Wisconsin lakes currently have no minimum length limit for largemouth bass, the opportunity to assess angler harvest selectivity for bass < 14-in TL exists, but would require that angler surveys be conducted on these lakes.
LITERATURE CITED


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Minnesota Department of Natural Resources (MNDNR) 1996. Lake Minnetonka Hennepin-Carver Counties, Summary of 1995-1996 winter (November 29-March 19) and 1996 summer (May15-October 31) angling (creel) survey.


Table 1.—Parameter estimates used in population models for largemouth bass in four northern Wisconsin lakes. General model parameters include initial abundance ($N_0$) with 95% confidence limits (in parentheses), instantaneous fishing mortality rates ($F$), density-independent ($\alpha$) and density-dependent parameters ($\beta$) and multiplicative process errors ($\varepsilon$) for Ricker stock-recruitment relationships. Sex-specific model parameters include estimates of asymptotic total length ($L_\infty$), Brody-Bertalanffy growth coefficients ($K$), and x-intercepts ($t_0$) from von Bertalanffy growth models, age at 50% maturity ($A_m$) and shape parameters ($r$) from age-at-maturity relationships and instantaneous natural mortality rates ($M$) estimated from Pauly (1980) models. Age-based parameter estimates for all lakes were based on estimates from sectioned otoliths with exception of Little John Lake, where dorsal spines were used for age estimation.

<table>
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<th>Sex</th>
<th>Parameter</th>
<th>Big Arbor Vitae</th>
<th>Big Sissabagama</th>
<th>Little John</th>
<th>Teal</th>
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<tr>
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<tr>
<td></td>
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<td>1.97</td>
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<tr>
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<tr>
<td>Maximum Age</td>
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Figure 1.—Temporal trends in statewide mean largemouth bass catch per mile for fish ≥ 8-in total length and fish ≥ 14-in total length from 1991 to 2011 (J. Hansen, WDNR, unpublished data). The relationship between catch per mile and year is significant ($P < 0.001$).
Figure 2.—Mean largemouth (closed diamonds) and smallmouth bass (open squares) angler catch per hour from creel surveys from 1990 to 2011 for lakes located within counties in northwest Wisconsin and the Ceded Territory (J. Hansen, WDNR, in press).
Figure 3.—Diagram of a simulation model used to predict effects of angler harvest regulations on largemouth bass populations in northern Wisconsin lakes, where \( i \) represents age and inputs are biological parameters from bass populations and instantaneous fishing mortality rate (\( F \)). All other symbols are defined in Methods.
Figure 4.—Sex-specific growth trajectories estimated from von Bertalanffy models for largemouth bass collected by boat electrofishing in May and June during 2012 or 2013 in four northern Wisconsin lakes (model parameters are reported in Table 1).
Figure 5.—Sex-specific maturity-at-age for largemouth bass collected by boat electrofishing in May and June during 2012 or 2013 in four northern Wisconsin lakes (model parameters are reported in Table 1).
Figure 6.—Sex-specific length-frequency distributions (1-in length intervals) for largemouth bass ≥ 8-in total length collected by boat electrofishing in May and June during 2012 or 2013 in four northern Wisconsin lakes.
Figure 7.—Sex-specific age-frequency distributions for largemouth bass ≥ 8-in total length collected by boat electrofishing in May and June during 2012 or 2013 from four northern Wisconsin lakes.
Figure 8.—Catch-curves of largemouth bass collected by boat electrofishing in May and June during 2012 or 2013 from four northern Wisconsin lakes.

Big Sissabagama Lake

\[ y = -0.1847x + 5.8639 \]

\[ R^2 = 0.2805 \]

\[ P = 0.0766 \]

Teal Lake

\[ y = -0.1908x + 5.9227 \]

\[ R^2 = 0.1348 \]

\[ P = 0.4179 \]

Big Arbor Vitae Lake

\[ y = -0.323x + 7.3341 \]

\[ R^2 = 0.3947 \]

\[ P = 0.0260 \]

Little John Lake

\[ y = -0.2616x + 4.8831 \]

\[ R^2 = 0.504 \]

\[ P = 0.0321 \]
Figure 9.—Abundance of largemouth bass populations in response to instantaneous fishing mortality ($F$) and alternative angling length limits in four Wisconsin lakes. The level of $F$ where reductions in abundance ≥ 25% (horizontal bar) and ≥ 50% (closed circles) occur are indicated. Reduction in abundance ≥ 25% did not occur under catch and release or an 18-in minimum length limit in any lake.
Figure 10.—Relative stock density of largemouth bass ≥ 15-in total length (RSD-15") in response to instantaneous fishing mortality ($F$) increases and alternative angling length limits in four Wisconsin lakes.
Figure 11.—Fecundity estimates for four largemouth bass using different numbers of 0.1-g subsamples used to determine that five 0.1-g subsamples were sufficient to estimate fecundity of an individual largemouth bass.
Figure 12.—Spawning potential ratio (SPR) of largemouth bass in response to instantaneous fishing mortality ($F$) and alternative angling length limits in three Wisconsin lakes.