Temporal Trends in Largemouth Bass Mortality, with Fishery Implications

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Abstract.—We reviewed estimates of annual exploitation (u) and total mortality (Z) for populations of largemouth bass Micropterus salmoides and used a simulation model to explore how temporal changes in u have influenced those populations. The review produced 32 estimates of u and 30 of Z spanning 51 years. Fishing mortality was roughly parabolic through time, with a mean of 0.35 for 1976–1989 and a mean of 0.18 for 1990–2003. Thus, average fishing mortality rates have declined by about one-half since about 1990. Total mortality declined with the decline in u, suggesting that changes in u caused lower overall total mortality rates. The evidence further suggests that the decline in u was caused by the voluntary release of fish by anglers rather than by changes in overall fishing effort. The simulation model showed that the decline in exploitation increased adult largemouth bass abundance but reduced the ability of size and bag regulations to improve population metrics owing to low rates of directed harvest. Discard mortality (i.e., the mortality of fish caught and released) would not negate the benefits of lower exploitation unless the mortality of fish caught and released was 0.3 or higher. Changes in angler behavior have substantially reduced fishing mortality for largemouth bass fisheries, which should be considered when developing management plans for this species and others with high rates of voluntary release.

Recreational fisheries are often considered less likely to suffer from recruitment overfishing than commercial fisheries (e.g., Walters and Maguire 1996; Cook et al. 1997; Jackson et al. 2001), but the impacts of recreational fishing can be severe. Post et al. (2002) showed that freshwater recreational fisheries can suffer from growth overfishing across broad geographic scales. Despite greater use of bag and size limits to lower exploitation over the past three decades (Radomski 2003), increasing angler effort in recreational fisheries still results in growth overfishing (Beard and Kampa 1999; Cox and Walters 2002). Identifying trends in fishing mortality for recreational fisheries is difficult owing to a lack of data to assess broad temporal or spatial scales (Post et al. 2002; Beard et al. 2003; Radomski 2003; Cooke and Cowx 2004).

Angler behavior also influences the potential for overfishing in recreational fisheries. Beard et al. (2003) found that angler effort declined as bag limits became more restrictive for walleye Sander vitreus in northern Wisconsin lakes. In contrast, voluntary release of fish that are legal to harvest has increased for many recreational fisheries (Quinn 1996). We found no studies evaluating whether observed shifts in angler behavior (e.g., Quinn 1996) can result in long-term trends in fish population metrics such as fishing or total mortality, and there is a need to evaluate broad spatial and temporal trends in mortality sources.

Largemouth bass Micropterus salmoides support some of the most popular recreational fisheries in North America, and some analyses have evaluated fishery responses to size limits across broad geographic scales. Beamesderfer and North (1995) used growth and natural mortality rates across largemouth bass populations to simulate potential fishery yield responses to harvest. Wilde (1997) conducted a meta-analysis of largemouth bass population responses to harvest restrictions. He concluded that minimum length limits did not influence fish abundance and size, whereas protective slot limits had some ability to increase both variables. His results were surprising because if fishing mortality were high, we would expect that protective size limits would influence fish abundance and size. Detecting effects of size limits can be difficult owing to

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variable recruitment, particularly when regulations are evaluated over a short time period (Allen and Pine 2000). Increases in fishing effort could also offset the benefits of protective size limits by increasing harvest on fish not protected by the size or bag limit (Cox and Walters 2002).

However, size limits would not increase fish size and abundance if overall exploitation is low and angler behavior has changed. For largemouth bass anglers in the 1990s, the harvest-associated aspects of fishing were apparently a relatively low motivation compared with factors such as the thrill of catching fish (Wilde and Ditton 1994; Wilde 1997). The lack of effects of size limits on largemouth bass populations identified by Wilde (1997) could result from high rates of voluntary release both before and after regulations were initiated.

In addition to the temporal changes in fishing mortality, any corresponding changes in total mortality have implications for management. If changes in exploitation have occurred, we would expect that total mortality rates would exhibit a corresponding change because fishing and natural mortalities appear to be additive for largemouth bass (e.g., Allen et al. 1998). However, the mortality of fish caught and immediately released or captured in tournaments could preempt this relation; such voluntary fishing-associated mortalities are typically not included in estimates of the exploitation rate (Allen et al. 2004). If instantaneous fishing mortality (F) and natural mortality (M) are additive, then changes in F should result in proportional changes in instantaneous total annual mortality (Z). Thus, evaluating how total mortality rates have changed with changes in fishing mortality could indicate the potential for nonharvest sources of fishing-associated mortality to act as cryptic sources of F.

We reviewed estimates of exploitation and total mortality for largemouth bass populations and evaluated how both variables have varied through time. Our objectives were to (1) evaluate the temporal trends in largemouth bass fishing and total mortality rates, (2) evaluate the influence of changing fishing mortality on total mortality rates, and (3) use a simulation model to explore how any changes in fishing mortality through time would influence largemouth bass populations.

**Methods**

Our review included the peer-reviewed literature and some state agency reports and graduate theses if they met our criteria for inclusion. Exploitation (u) was defined as the fraction of the vulnerable stock that was harvested by anglers. Exploitation estimates were derived by (1) estimated harvest divided by estimated vulnerable stock size, (2) tagging studies where anglers returned tagged fish, and (3) telemetry studies. Tagging studies were not included in our analyses if they did not correct for angler nonreporting of tags, tag loss, and tagging mortality or if the authors failed to justify these potential biases as minimal owing to the circumstances at each water body. Values of u from water bodies with more than 1 year of estimates were averaged if they were within 0.10, but considered separately if they differed by more than this value. Total mortality rates were estimated either with tagging methods or changes in abundance at age, either via catch curves or from following cohorts through time. Mortality expressions used in this paper are shown in Table 1.

<table>
<thead>
<tr>
<th>Expression</th>
<th>Definition</th>
<th>Rate type</th>
<th>Relations to other rates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Z</td>
<td>Total mortality</td>
<td>Instantaneous</td>
<td>Z = −log(1 − A)</td>
</tr>
<tr>
<td>F</td>
<td>Fishing mortality</td>
<td>Instantaneous</td>
<td>F = −log(1 − u)</td>
</tr>
<tr>
<td>M</td>
<td>Natural mortality</td>
<td>Instantaneous</td>
<td>Z = F + M</td>
</tr>
<tr>
<td>u</td>
<td>Fishing mortality</td>
<td>Finite</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>Total mortality</td>
<td>Finite</td>
<td></td>
</tr>
<tr>
<td>d</td>
<td>Discard mortality</td>
<td>Finite</td>
<td></td>
</tr>
</tbody>
</table>

We used lowess regression to evaluate the temporal trends in exploitation rates across largemouth bass populations. The lowess regression fits a locally weighted polynomial to the data and is useful for identifying trends in data where no preconceived model (e.g., linear or quadratic) is appropriate (Cleveland and Devlin 1988). We used SAS (2002) to fit the model and a selection procedure based on the Akaike information criterion corrected for small sample size (AICc) to estimate the smoothing parameter q (SAS 2002). The smoothing parameter, q, controls the flexibility of the regression function and is a number between (d + 1)/n and 1, with d denoting the degree of the local polynomial. The lowess regression was used to identify trends in exploitation through time. To assess how temporal trends in u varied with geographical region, we grouped the estimates into four regions:
southern (Alabama, Georgia, Florida, Tennessee, and Texas), western (California and Idaho), Midwestern (Iowa, Michigan, and Wisconsin), and northeastern (Connecticut).

To compare the average values of \( u \) between time periods, we used a bootstrap routine written for use in Excel (Poptools [www.cse.csiro.au/poptools]). We resampled the \( u \) estimates across all regions for two time periods and obtained a mean. Time periods were selected by evaluating the temporal trends in \( u \) and considering distinct periods of change. The resampling approach was repeated 10,000 times, which provided a bootstrap mean and 95\% confidence intervals for \( u \) from each time period.

To evaluate how changes in \( F \) could have influenced \( Z \), we evaluated the relationship between fishing and total mortality. Estimates of finite annual mortality (\( A \)) were transformed to \( Z \) as per Table 1. Estimates of exploitation were used to predict \( F \) as \(-\log(1 - u)\) (Table 1) from Hilborn and Walters (1992). This transformation of \( u \) to \( F \) assumes that fishing and natural mortality occur separately during the year (i.e., that there are seasonal fisheries and periods of natural death), but the approximation is typically satisfactory for evaluating how \( F \) varies across populations even where fishing and natural mortality occur simultaneously.

We used linear regression to evaluate the relationship between \( Z \) and \( F \) across populations. Our expectation was that the slope of the relationship between \( Z \) and \( F \) should be close to 1 (i.e., additive fishing and natural mortalities).

We constructed an age-structured population model to assess how observed changes in \( F \) would influence largemouth bass fisheries. The model was an equilibrium yield analysis adapted from Botsford and Wickham (1979) and Botsford (1981a, 1981b) and summarized by Walters and Martell (2004:56).

We used average growth rates from Beamesderfer and North (1995), derived from the von Bertalanffy growth equation

\[
\text{total length (TL [mm])} = 580[1 - e^{-0.2 \times (\text{age} + 0.24)}].
\]

Fishing mortality was varied according to values found in this review and the estimate of \( M \) from the intercept of a regression of \( Z \) on \( F \) for this study. Discard mortality (i.e., mortality of fish caught and released below the minimum size limit) was simulated by subjecting fish below a range of minimum length limits to \( F \times d \), where \( d \) is the discard mortality rate (Table 1). We used 1,000 recruits to age 1 to predict fish numbers at age per thousand recruits. The model was constructed in Microsoft Excel and was used to predict how the population abundance of largemouth bass would vary with changes in \( F \), minimum legal size, and discard mortality. We simulated minimum length limits ranging from no limit (fish vulnerable to harvest at 200 mm TL) to 450 mm TL and discard mortality rates ranging from 0 to 0.3.

**Results**

We obtained 36 estimates of exploitation and 34 corresponding total mortality estimates from 11 U.S. states and Puerto Rico (Table 2). Estimates made by Kimsey (1957), Van Woert (1980), and Ager (1984) were excluded from further analysis because they did not correct for tag loss, tagging mortality, or non-reporting of tags (Table 2). Ager (1979) did not correct for the nonreporting rate, but we used his estimates because tags were rewarded and could be redeemed at the boat ramp; thus, he believed that nonreporting was minimal. We excluded Waters et al. (2005) because their estimates were from a reservoir in Puerto Rico where angler motivation regarding harvest could differ from the other systems and because the reservoir was closed during a portion of their sample year owing to a hurricane. These exclusions resulted in 32 estimates of exploitation and 30 corresponding estimates of total annual mortality.

The time span of the estimates was 51 years (1953–2003), \( u \) averaging 30\% and \( A \) averaging 57\% over this period. The exploitation rate ranged from 0.07 at Sam Rayburn Reservoir, Texas, in 2003 to 0.58 at Chambers Reservoir, Alabama, in 1979 (Table 1). The range in \( A \) was from 0.24 at Browns Lake, Wisconsin, in 1953 to 0.91 at Tobsoskee Reservoir, Georgia, in 1977 (Table 2).

The temporal trend in exploitation appeared roughly parabolic (Figure 1). Exploitation estimates were relatively low in the 1950s–1960s, highly variable in the 1970s–1980s, and low and relatively precise (all below 0.2) since 1990, except for the Gardner Lake, Connecticut, estimate from 2001 (Figure 1). The \( AIC_c \) procedure selected a smoothing parameter of 1, and year explained 31\% of the variation in \( u \) (Figure 1). The parabolic trend was not dependent on region, as removal of any region would yield the same general pattern (Figure 1). The total number of exploitation estimates peaked in the 1970s through the 1980s (\( N = 18 \) water bodies), whereas the number of estimates from 1990 to 2003 was considerably lower (\( N = 7 \) water bodies).

We grouped estimates of \( u \) into two 13-year periods (1976–1989 and 1990–2003) for the bootstrap procedure. The bootstrapping routine found a mean \( u \) of 0.35 for the 1976–1989 time period with 95\% confidence intervals of 0.26–0.44. For the 1990–2003 period, the
bootstrap mean $u$ was 0.18 with 95% confidence intervals of 0.11–0.27. Although there was substantial variation in the exploitation estimates in the 1970s and 1980s, the bootstrapping procedure suggested that average fishing mortality rates have declined by about one-half since 1990.

As expected, estimates of $Z$ were positively related to $F$ ($P < 0.01, r^2 = 0.48$) for the 30 cases where both

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**Table 2.** Summary of total annual mortality ($A$), instantaneous total mortality ($Z$), and annual exploitation rate ($u$) estimates for largemouth bass by lake and year. Samples collected over consecutive years were averaged.

<table>
<thead>
<tr>
<th>Lake; state</th>
<th>Year(s)</th>
<th>$A$</th>
<th>$Z$</th>
<th>$u$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whitmore; Michigan</td>
<td>1953</td>
<td>0.42</td>
<td>0.54</td>
<td>0.22</td>
<td>Cooper and Schafer (1954)</td>
</tr>
<tr>
<td>Clear; California</td>
<td>1953</td>
<td>0.70</td>
<td>1.20</td>
<td>0.35</td>
<td>Kimsey (1957)</td>
</tr>
<tr>
<td>Browns; Wisconsin</td>
<td>1956</td>
<td>0.24</td>
<td>0.27</td>
<td>0.12</td>
<td>Mraz and Threinen (1957)</td>
</tr>
<tr>
<td>Sutherland; California</td>
<td>1956–1959</td>
<td>0.72</td>
<td>1.27</td>
<td>0.43</td>
<td>La Faunce et al. (1964)</td>
</tr>
<tr>
<td>Sugarloaf; Michigan</td>
<td>1962</td>
<td>0.70</td>
<td>1.20</td>
<td>0.35</td>
<td>Cooper and Latta (1962)</td>
</tr>
<tr>
<td>Merle Collins; California</td>
<td>1965–1969</td>
<td>0.82</td>
<td>1.71</td>
<td>0.55</td>
<td>Rawstron and Hashagen (1972)</td>
</tr>
<tr>
<td>Center Hill; Tennessee</td>
<td>1975–1976</td>
<td>0.58</td>
<td>0.87</td>
<td>0.37</td>
<td>Yeager and Van Den Avyle (1979)</td>
</tr>
<tr>
<td>Mid Lake; Wisconsin</td>
<td>1976</td>
<td>0.68</td>
<td>1.14</td>
<td>0.45</td>
<td>Van Woert (1980)</td>
</tr>
<tr>
<td>Ocmulgee River; Georgia</td>
<td>1980</td>
<td>0.32</td>
<td>0.39</td>
<td>0.11</td>
<td>Coomer and Holder (1984)</td>
</tr>
<tr>
<td>Thompson; Idaho</td>
<td>1981</td>
<td>0.62</td>
<td>0.97</td>
<td>0.48</td>
<td>Reiman (1982)</td>
</tr>
<tr>
<td>Medicine; Idaho</td>
<td>1981</td>
<td>0.65</td>
<td>1.05</td>
<td>0.49</td>
<td>Reiman (1982)</td>
</tr>
<tr>
<td>Ferman; Idaho</td>
<td>1981</td>
<td>0.82</td>
<td>1.71</td>
<td>0.72</td>
<td>Reiman (1982)</td>
</tr>
<tr>
<td>Rum Creek; Georgia</td>
<td>1984</td>
<td>0.88</td>
<td>3.12</td>
<td>0.19</td>
<td>Ager (1984)</td>
</tr>
<tr>
<td>Bartlett’s Ferry; Georgia</td>
<td>1983–1986</td>
<td>0.79</td>
<td>1.56</td>
<td>0.14</td>
<td>Keefer (1988)</td>
</tr>
<tr>
<td>Walter F. George; Georgia</td>
<td>1983–1986</td>
<td>0.56</td>
<td>0.82</td>
<td>0.25</td>
<td>Keefer (1988)</td>
</tr>
<tr>
<td>Seminole; Georgia</td>
<td>1983–1986</td>
<td>0.58</td>
<td>0.87</td>
<td>0.14</td>
<td>Keefer (1988)</td>
</tr>
<tr>
<td>Blackshear; Georgia</td>
<td>1983–1986</td>
<td>0.48</td>
<td>0.65</td>
<td>0.09</td>
<td>Keefer (1988)</td>
</tr>
<tr>
<td>Lanier; Georgia</td>
<td>1986</td>
<td>0.43</td>
<td>0.56</td>
<td>0.16</td>
<td>Weaver (1989)</td>
</tr>
<tr>
<td>Escambia River; Florida</td>
<td>1986–1988</td>
<td>0.71</td>
<td>1.24</td>
<td>0.42</td>
<td>Keuse (2002)</td>
</tr>
<tr>
<td>Brown; Iowa</td>
<td>1988</td>
<td>0.65</td>
<td>1.05</td>
<td>0.35</td>
<td>Pilto and Bonneau (1992)</td>
</tr>
<tr>
<td>Sunfish; Iowa</td>
<td>1988</td>
<td>0.53</td>
<td>0.75</td>
<td>0.47</td>
<td>Pilto and Bonneau (1992)</td>
</tr>
<tr>
<td>Methodist; Iowa</td>
<td>1989</td>
<td>0.55</td>
<td>0.80</td>
<td>0.15</td>
<td>Pilto and Bonneau (1992)</td>
</tr>
<tr>
<td>Norwegian; Iowa</td>
<td>1989</td>
<td>0.46</td>
<td>0.62</td>
<td>0.41</td>
<td>Pilto and Bonneau (1992)</td>
</tr>
<tr>
<td>Minnesota Slough; Iowa</td>
<td>1989</td>
<td>0.58</td>
<td>0.87</td>
<td>0.22</td>
<td>Pilto and Bonneau (1992)</td>
</tr>
<tr>
<td>Conway chain; Florida</td>
<td>1991</td>
<td>0.52</td>
<td>0.73</td>
<td>0.17</td>
<td>Renfro et al. (1999)</td>
</tr>
<tr>
<td>Winter Park chain; Florida</td>
<td>1991</td>
<td>0.50</td>
<td>0.69</td>
<td>0.16</td>
<td>Renfro et al. (1999)</td>
</tr>
<tr>
<td>Norris; Tennessee</td>
<td>1996–1997</td>
<td>0.19</td>
<td>1.24</td>
<td>0.42</td>
<td>Keuse (2002)</td>
</tr>
<tr>
<td>Lucchetti; Puerto Rico</td>
<td>1997</td>
<td>0.59</td>
<td>0.89</td>
<td>0.38</td>
<td>Waters et al. (2005)</td>
</tr>
<tr>
<td>Rodman Reservoir; Florida</td>
<td>2001</td>
<td>0.48</td>
<td>0.65</td>
<td>0.11</td>
<td>Henry (2003)</td>
</tr>
<tr>
<td>Mansfield; Connecticut</td>
<td>2001–2002</td>
<td>0.38</td>
<td>0.48</td>
<td>0.12</td>
<td>Edwards et al. (2004)</td>
</tr>
<tr>
<td>Gardner; Connecticut</td>
<td>2001</td>
<td>0.41</td>
<td>0.53</td>
<td>0.48</td>
<td>Edwards et al. (2004)</td>
</tr>
<tr>
<td>Gardner; Connecticut</td>
<td>2002</td>
<td>0.41</td>
<td>0.53</td>
<td>0.11</td>
<td>Edwards et al. (2004)</td>
</tr>
<tr>
<td>Sam Rayburn; Texas</td>
<td>2003</td>
<td>0.37</td>
<td>0.46</td>
<td>0.07</td>
<td>Driscoll et al. (2007)</td>
</tr>
</tbody>
</table>

* Not included in Figures 1 and 2 (see text).
variables were measured (Figure 2). The slope of the relation was 1.11 and was not significantly different from 1.0 ($P = 0.22$). This suggests that $F$ and $M$ were indeed additive, as previously reported in a review for largemouth bass (Allen et al. 1998).

The intercept of the regression in Figure 2 (0.49) provided an estimate of the average value of $M$, the instantaneous natural mortality rate across populations. Estimates of $M$ found by subtracting $F$ from $Z$ were highly variable across studies. The mean $M$ was 0.55 across 29 studies, and values ranged from 0.09 to 1.59. An $M$ estimate was not possible for Gardner Lake, Connecticut, in 2001 because the predicted fishing mortality in that year was higher than the estimate of total mortality (Table 1). We found a wide range of values for $M$ across largemouth bass populations, which would influence the population responses to management actions if $M$ is actually that variable. However, we suspect that $M$ is in fact not all that variable, but do not have a method for estimating how much the $M$ estimates should vary by chance alone owing to sampling or estimation variability associated with estimates of both $Z$ and $F$.

For the equilibrium yield model we simulated a range of fishing mortalities from 0 to 0.5 and used the bootstrap mean $u$ from 1976 to 1989 ($u = 0.35$, $F = 0.45$) rather than the mean from 1990 to 2003 ($u = 0.18$, $F = 0.2$) as a guide for the average estimated change in fishing mortality and population abundance. Although $u$ declined from the first period to the second, we assumed that the decline was due to the voluntary release of fish rather than reductions in fishing effort. Thus, we modeled the overall capture rate ($F_o$) as 0.45 (as per 1976–1989) for both time periods and used a lower harvest rate (0.2) for the second time period (1990–2003). For the second time period we modeled total mortality as

$$Z = F + (F_o - F)d + M,$$

where $d$ is the discard mortality rate (Table 1). This simulated a scenario where the decline in overall fishing mortality would be offset by discard deaths that occur at the rate of $(F_o - F)d$.

The model results indicated that the decline in fishing mortality since the late 1980s would increase the number of adult (≥age-4) fish in the population (Figure 3). If discard mortality was nil, then the model predicted that the decline in $F$ would increase the number of age-4 and older fish from about 490 to 540 with a 350 mm minimum length limit (MLL). At a discard mortality rate of 0.3, the same MLL caused adult abundance to increase from about 420 to 470. Thus, the model predicted that the reduction in $F$ would improve adult fish abundance in the population for a given level of discard mortality (Figure 3). However, the model showed that discard mortality exceeding about 0.3 could negate benefits of lower overall $F$ (Figure 3).

The model also indicated that the reduction in $F$ would influence the ability of fishery managers to detect largemouth bass population responses to minimum length limits. Increases in fish abundance via minimum length limits were less likely if $F$ was low (0.2) than high (0.45) under all scenarios (Figure 3). For example, for a discard mortality rate of 0.1, increasing the minimum size limit from 300 to 400 mm TL caused the number of age-4 and older fish to increase from about 400 to 525 if $F$ was high (1976–1989, Figure 3). Conversely, if $F$ was low (1990–2003), the same increase in minimum size limit resulted in increases from 470 to 550. Thus, expected benefits in fish abundance via minimum length limits would be reduced today relative to $F$ values from the mid 1980s owing to lower overall fishing mortality. Nevertheless, the model also predicted higher abundance for the recent period of lower $F$, thus making length limits less important for reducing fishing mortality in largemouth bass fisheries.

**Discussion**

The decline in exploitation since the mid 1970s was most likely caused by more voluntary releases of fish that were legal to harvest rather than less fishing effort. About 95% of U.S. state conservation agencies reported increasing voluntary release of largemouth bass that were legal to harvest in the mid-1990s (Quinn 1996). Similarly, Noble (2002) found that about 94% of U.S. and Canadian conservation agencies reported increased voluntary release of black basses *Micropterus* spp. through time. Although the total number of angler-days in the United States has declined slightly through time, the total fishing effort for black basses has remained relatively stable at 10–12 million anglers according to three national surveys from 1991 to 2001 (J. Leonard, U.S. Fish and Wildlife Service, personal communication). Myers et al. (2008, this issue) documented large increases in the voluntary release rates of largemouth bass legal to harvest in Florida and Texas, from 10% in the late 1970s to over 80% for some water bodies in the early 2000s in Texas and Florida. Our study provides evidence that these changes in angler behavior caused a substantial decline in fishing and total mortality for largemouth bass.

However, we found evidence that some largemouth bass populations still incur high fishing mortality. Exploitation at Gardner Lake, Connecticut, was 0.48 in 2001, but low in 2002 (0.11). Edwards et al. (2004) found that largemouth bass harvest in 2001 at Gardner
Lake was high owing to harvest from ice fishing anglers. Interestingly, the \( u \) estimates were low (0.12) for Mansfield Lake, Connecticut, in both years despite higher angler effort in 2001 at both lakes during the ice season (Edwards et al. 2004). The Gardner Lake example shows that largemouth bass fishing mortality can still range widely depending on the lake and year, with high \( u \) values estimated in one year and not another at this system.

Voluntary release rates have also been increasing for other fisheries, but the trends vary across species. Margenau and Petchenik (2003) found that 90% of surveyed muskellunge \( Esox masquinongy \) anglers voluntarily released fish legal to harvest. Fayram (2003) documented increasing voluntary release rates for muskellunge fisheries in northern Wisconsin through time, but regulations were required to increase the overall release rates for walleye fisheries because anglers sought walleye as a food fish. Coble (1988) found a strong relationship between fishing effort and \( u \) for bluegill \( Lepomis macrochirus \) in Wisconsin lakes, indicating harvest-oriented bluegill fisheries.

The observed temporal declines in \( u \) would lessen the responses of largemouth bass populations to length limits and make detecting the effects of length limits more difficult. Environmental effects on recruitment can make changes in population metrics owing to size limits difficult to discern (Buynak et al. 1991). Allen and Pine (2000) found that moderate changes in population abundance would be difficult to detect because of the variable recruitment for largemouth bass fisheries, and the change in mean \( u \) that we observed would reduce fishery managers’ ability to significantly alter largemouth bass abundance and size structure with size limits. However, the lower \( u \) since 1990 suggests that fewer largemouth bass fisheries would
require length limits to prevent overfishing because total mortality estimates have also declined. These results could contribute to the lack of largemouth bass population responses to regulations identified by Wilde (1997).

The positive relationship between $F$ and $Z$ suggests that lower fishing mortality through time has caused coincident declines in total mortality. If the fishing effort in largemouth bass fisheries has remained about the same and voluntary releases have caused the lower $F$ through time, this implies that cryptic sources of $F$ (such as catch-and-release and tournament-associated mortality) have not been large. In our analyses, $Z$ declined approximately as expected as $u$ declined, suggesting that discard mortality has not negated the benefits of lower harvest rates.

However, with increased emphasis on catch-and-release fishing for black basses, mortality sources other than harvest have been a management concern (Noble 2002). Tournament-associated mortality has been a concern of management agencies because fish brought to judging stations may incur high mortality even if they are released alive (reviewed by Wilde 1998). Field studies that have measured tournament mortality impacts at the population level have generally indicated low impacts (Kwak and Henry 1995; Neal and Lopez-Clayton 2001; Edwards et al. 2004; Driscoll et al. 2007). Allen et al. (2004) used a simulation model to show that tournament-associated mortality rates could cause population declines if harvest levels were also high, but at low exploitation rates the effects would probably be minimal. We found evidence that exploitation was generally low since 1990, suggesting that tournament mortality is unlikely to cause population declines for most water bodies. Nevertheless, under a scenario of increasing tournament catch and low $u$, the fraction of total fishing mortality resulting from tournaments could be high. More studies are needed that separate all components of $F$ for fisheries with high voluntary release rates, including not only harvest but also catch-and-release and tournament-associated effects (see Driscoll et al. 2007).

In addition to the potential effects of tournaments on adult fish abundance, the practice of catching black basses from spawning beds can reduce nest success, even if fish are released immediately or after transport to tournament judging stations (Philipp et al. 1997; Cooke et al. 2000; Suski and Philipp 2004). The population implications of nest failures from catch-and-release angling have not been determined. However, regulations such as closed seasons or protected areas (Suski et al. 2002) that are intended to promote nest success for black basses should be accompanied with estimates of exploitation to evaluate all components of mortality influencing black bass fisheries. If $u$ is high, more anglers would keep their fish and not allow the fish to spawn again. With lower $u$, the population could incur reduced nest success via catch-and-release fishing (e.g., Philipp et al. 1997), but lower adult mortality rates would presumably allow repeated spawning of adults. This trade-off in mortality rates between different life stages warrants evaluation to allow informed regulation choices.

Our estimate of $M$ was 0.49 across largemouth bass populations, which is similar to the 0.42 reported by Beamesderfer and North (1995). There was a large range in estimates of $M$ across populations, which probably resulted from both real variation in $M$ and sampling variation around estimates of both $Z$ and $F$. Catch curves were used to estimate $Z$ in most of the studies we reviewed, and factors such as variable recruitment and sampling biases can strongly influence catch curve estimates (Ricker 1975). Despite this uncertainty we were able to detect a clear positive relationship between $Z$ and $F$ that was similar to the expected value (i.e., with a slope near 1).

We believe that the frequency of exploitation estimates through time reflects a shift in management agency priorities. The number of studies estimating $u$ was very high during the 1970s and 1980s but has been much lower since 1990 (Figure 1). Two of the most recent estimates of $u$ (Edwards et al. 2004; Driscoll et al. 2007) are from studies intended to measure tournament mortality rather than fishing mortality. The lower number of estimates from 1990 to 2003 could result because management agencies and researchers do not perceive harvest of largemouth bass to be a fishery constraint.

However, our results do not imply that fishing mortality does not negatively affect the socioeconomic value of fisheries, even if overall exploitation rates are usually low. Henry (2003) found that although overall $u$ was low, exploitation of the largest fish was two to three times higher. Most studies in this review did not report how $u$ changed with fish size, but size-selective $u$ could still result in negative effects on fisheries, particularly when management goals include trophy fisheries. Research regarding fishing mortality for largemouth bass and other species with high voluntary release rates will require much more detailed methods in the future. The components of $F$ are changing for these species and cryptic sources of $F$ such as catch-and-release and tournament mortality may make up a larger fraction of the total $F$. Nevertheless, declines in $F$ were also associated with reduced total mortality, showing that changes in angler behavior have lowered fishing mortality for largemouth bass populations.
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References


Ager, L. M. 1984. Dynamics of the largemouth bass population in Rum Creek Reservoir. Georgia Department of Natural Resources, Federal Aid to Fish Restoration, Project F-33, Atlanta.


Jackson, J. B. C., and eighteen coauthors. 2001. Historical


