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Factors Affecting the Vulnerability to Angling of Nesting Male Largemouth and Smallmouth Bass

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Abstract.—Some, but not all, jurisdictions in North America have regulations in place designed to protect nesting male largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu* from angling. The underlying assumption that brood-guarding males are particularly vulnerable to angling, however, is untested. In this study, we quantified the vulnerability of brood-guarding largemouth bass and smallmouth bass to angling and determined the factors that influenced that vulnerability. For this, male largemouth bass and smallmouth bass guarding newly spawned eggs were located by snorkel survey. The aggression of these males towards a brood predator was quantified, the male's susceptibility to angling lures was assessed, and the quantity of eggs in his nest and his size were recorded. Male largemouth and smallmouth bass were quite vulnerable to angling while guarding their nests, 70% of nesting male smallmouth bass and 54% of nesting male largemouth bass being hooked during the experimental angling trials. The level of aggression shown by nesting males of both species towards the brood predator model was significantly influenced by the quantity of eggs in his nest. This relationship was true regardless of male size, although larger males of both species typically received a greater quantity of eggs during a reproductive attempt. Furthermore, vulnerability to angling correlated positively with the quantity of eggs in a male's nest. Thus, the males that had the largest broods and the greatest potential to contribute to annual recruitment were the most likely to be caught by anglers, indicating that angling for nesting bass during the brood-guarding period has the potential to negatively impact bass populations.

Largemouth bass *Micropterus salmoides* and smallmouth bass *M. dolomieu* are two of the most popular and economically important sport fish in North America (Department of Fisheries and Oceans Canada 1998; Pullis and Laughland 1999). In response, management agencies have implemented numerous regulations to protect and enhance bass fisheries (e.g., daily harvest limits, length limits, and closed areas; Noble and Jones 1999; Noble 2002). These regulations are often effective in preventing overexploitation (Sztramko 1985; Wilde 1997). In some jurisdictions, seasonal closures during the brood-guarding period, when bass may be most vulnerable to angling, are added to provide additional protection (Quinn 2002).

Like other centrarchids, male largemouth bass and smallmouth bass excavate shallow, bowl-like nests in the littoral zones of lakes and rivers, typically in late spring (Breder 1936; Coble 1975; Heidinger 1975). Following nest construction, females are courted to the nest site, and once spawning is completed, the male remains alone at the nest site to provide sole parental care for the developing brood (Breder 1936; Coble 1975; Heidinger 1975). Parental care can last up to 5 weeks and includes both fanning the nest to provide oxygen to the eggs and larvae (Coble 1975; Heidinger 1975; Ridgway 1988) and defense against predators (Ridgway 1988; Ongarato and Snucins 1993; Suski et al. 2003). Defense of a brood can occur in many forms, and Breder (1936) documented that in centrarchids, brood defense can occur in the form of ''yawning'' displays as well as through chasing potential intruders from the nest area.

If a nesting male largemouth bass or male smallmouth bass is removed from his nest through angling, his brood is left defenseless against predators during his absence (Neves 1975). If that male is harvested, rapid and total brood loss is a likely outcome. If the male is released, variable levels of brood loss are possible, depending upon the conditions of release (Philipp et al. 1997). Reduction in brood size by predation while a male is absent from his nest increases the likelihood of premature abandonment (Suski et al. 2003) and may result

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in zero reproductive output for that spawning event. Following the return of the male to the nest, the physiological impairment that accompanies a catch-and-release angling event can reduce the level of defense provided to the brood (Kieffer et al. 1995; Cooke et al. 2000; Suski et al. 2003). Regulations closing bass fisheries during spawning season are promulgated under the assumption that bass are more vulnerable to angling during this stage, but this assumption has not been validated (but see Shuter et al. 1980; Philipp et al. 1997; Suski et al. 2003).

In this study, we quantified the vulnerability to angling of nesting male largemouth bass and smallmouth bass and determined which factors affect this vulnerability. We also examined the interrelationships among four different characteristics of brood-guarding male largemouth bass and smallmouth bass: total length (TL), mating success, aggression toward brood predators, and vulnerability to angling.

Methods

Study sites.—We collected data on nesting male largemouth bass and smallmouth bass from seven lakes (Loughborough Lake, Sand Lake, Lake Opinicon, Warner Lake, Bob's Lake, Devil Lake, and Buck Lake) in southeastern Ontario during May and June of 1999 and 2000. All sites contained self-sustaining sympatric populations of largemouth bass and smallmouth bass, except Warner Lake, which contained only largemouth bass.

Field techniques.—We used snorkel surveys in the littoral zone of the study lakes to locate nesting male bass guarding newly spawned eggs (<3 d old). Upon discovery of a nesting bass, we marked each nest with an individually numbered plastic tag, drew the location of the nest on a map of the study site, visually estimated the size of the nest-guarding male, recorded the male's mating success (a visual, relative approximation of eggs in a nest, with categories ranging from a low of 1 to a high of 5; Kubacki 1992; Philipp et al. 1997; Suski et al. 2002), noted the depth of the nest, and checked for the presence of any hookwounds on the male. A hookwound is a bruise or small laceration that develops around the mouth of a bass following a catch-and-release angling event. Most hookwounds remain visible for about 2 weeks, making hookwounds from previous years undetectable. We considered the presence of a hookwound on a male bass to be indicative of a recent catch-and-release angling event (Suski et al. 2002; Suski et al. 2003) and did not include males with hookwounds in the study.

To assess the level of antipredator aggression, we presented each nesting male with a model of a brood predator. The model was a resin-coated photograph of an immature bluegill *Lepomis macrochirus* (TL ≅ 150 mm) mounted on a Plexiglas backing and attached to a 1.5-m metal rod (Coleman et al. 1985; Suski et al. 2003). We ''swam'' the model in the center of a male's nest for 30 s in a manner that simulated egg predation, and we quantified three aggressive behaviors of the nesting male (Suski et al. 2003). A ''yawn'' occurred when a male opened his mouth and flared his branchiostegal membranes, a ''rush'' occurred when a male swam quickly toward the model but did not strike it, and a ''hit'' occurred when a male made physical contact with the model by striking or biting it. Because these actions were mutually exclusive events (e.g., males could not yawn and rush at the same time), we summed the occurrences of all three behaviors as the total number of antipredator behaviors (TAB score) performed by each nesting male.

Following aggression tests, the snorkeler made maps of the study site, which were used to direct anglers in a boat to all of the nesting male bass targeted for antipredator aggression. After locating the nest, we positioned the boat several meters from the male's nest and took care to not disturb the male. We then quantified the susceptibility of the male to three different fishing lures. Anglers presented each male with two casts of a hard plastic, silver stick bait (approximately 10 cm in length), followed by two casts of a black plastic worm (approximately 15 cm in length) rigged ''Texas style,'' followed by two casts of a 1/8-oz (3-g) lead jig head with an 8-cm white plastic Mister Twister jig body. The order of lure presentation was identical for all males, and three different lures were used to increase the likelihood of eliciting a response from a nesting male. Valid casts were those within 1 m of the nest; other casts were not counted, and few casts were disqualified. If a nesting male responded to the presence of the lure by attacking or ingesting it, we attempted to hook and land the fish. For each cast, we noted if the male bass made contact with the lure, whether the male was hooked, and whether it was landed in the boat. Some bass did not respond to any lure presentations. Once landed, we unhooked, measured (TL to the nearest millimeter), and released males above their nests less than 2 min after landing. The

TABLE 1.—Analysis of covariance comparing the total aggressive behaviors (TAB score) of nesting male smallmouth and largemouth bass with differing egg scores. Male size (total length [TL] in millimeters) is the covariate in the model; degrees of freedom are indicated in parentheses.

	Smallmouth bass		Largemouth bass	
	F	*P*	*F*	*P*
Egg score	42.1 (4, 204)	<0.0001	27.0 (4, 80)	<0.0001
TL (mm)	0.04 (1, 204)	0.8	0.5 (1, 80)	0.5
TL × egg score	1.1 (4, 204)	0.4	0.7 (4, 80)	0.6

time between nest location and lure presentation was less than 2 h.

Statistical testing.—For both species, we assessed the relationship between egg score and TAB score of a particular male using an analysis of covariance (ANCOVA) with male size as the covariate in the model (Sokal and Rohlf 1995). We assessed the relationship between egg score and male size directly using nonparametric Spearman rank correlation, and examined the relationship between the TL of angled males and our visual length approximations of the same nesting male using regression analyses (Zar 1999). We detected differences across the proportion of males striking lures based on egg score using contingency table analysis, and we assessed differences between individual proportions using multiple comparisons for proportions (Zar 1999). We made comparisons of TAB scores as they related to categorical angling response using a Kruskal–Wallis test followed by a nonparametric posthoc test to detect differences between categories (Zar 1999). All statistical analyses were performed using JMPIN 4.0 (Sall et al. 2001), except for comparisons of proportions and nonparametric posthoc tests, which we performed by entering formulae into a spreadsheet on a personal computer. The level of significance (α) for all tests was 0.05, and all data are presented ± SE where appropriate.

Results

Although both species of brood-guarding male bass were aggressive toward angled lures during this study, smallmouth bass were more aggressive than largemouth bass. Of the 214 male smallmouth bass that received lure presentations, 70% (149) were hooked, and 43% hit the silver stick bait on the first cast. In contrast, 49 of the 90 nesting largemouth bass tested (54%) were hooked, and only 34% hit the silver stick bait on the first cast.

When the visual size approximations of a nesting male made by snorkelers were compared with measured TL, the two variables were significantly related with a large coefficient of determination (regression analysis: $r^2 = 0.89$, $N = 110$, $F = 881.1$, $P < 0.001$). This allowed us to use the visually estimated TL of all males tested in several analyses. The response of a male to the predator model was strongly associated with his egg score as bass of both species with higher egg scores were significantly more aggressive towards the predator model, regardless of size (ANCOVA; Table 1). Typically, however, larger nesting males had greater numbers of eggs in their nests than did smaller males for both largemouth bass ($r = 0.39$, $N = 90$, $P < 0.0001$; Figure 1) and smallmouth bass ($r = 0.41$, $N = 214$, $P < 0.0001$; Figure 1).

Male bass with egg scores of 3 or more were significantly more likely to hit a lure during the six casts than males with egg scores or 2 or less (contingency table analysis: $\chi^2_{\text{largemouth bass}} = 32.8$, $\chi^2_{\text{smallmouth bass}} = 32.8$, $n_{\text{largemouth bass}} = 90$, $n_{\text{smallmouth bass}} = 214$, df = 4, $P < 0.05$; Figure 2,). Finally, both the male largemouth bass (Kruskal–Wallis test: $\chi^2_{2,120} = 66.0$, $P < 0.0001$; nonparametric posthoc test: $P < 0.05$; Figure 3) and the male smallmouth bass (Kruskal–Wallis test: $\chi^2_{2,307} = 110.2$, $P < 0.0001$; nonparametric posthoc test: $P < 0.05$; Figure 3) that responded to angled lures had significantly higher aggression toward brood predators (TAB scores) than males that did not respond to lures.

Discussion

Brood guarding by males is a life history trait common to all members of the family Centrarchidae (Breder 1936), its purpose being to increase offspring survival (Sargent and Gross 1986; Sargent 1997). A positive relationship between brood size and parental aggression towards brood predators exists across many different taxa, including both fish (e.g., bluegill [Coleman et al. 1985], threespine stickleback *Gasterosteus aculeatus* [Pressley 1981], and Central American cichlid *Aequidens coeruleopunctatus* [Carlisle 1985]) and birds (see Montgomerie and Weatherhead 1988). In the current study, increases in brood size for both largemouth bass and smallmouth bass re-

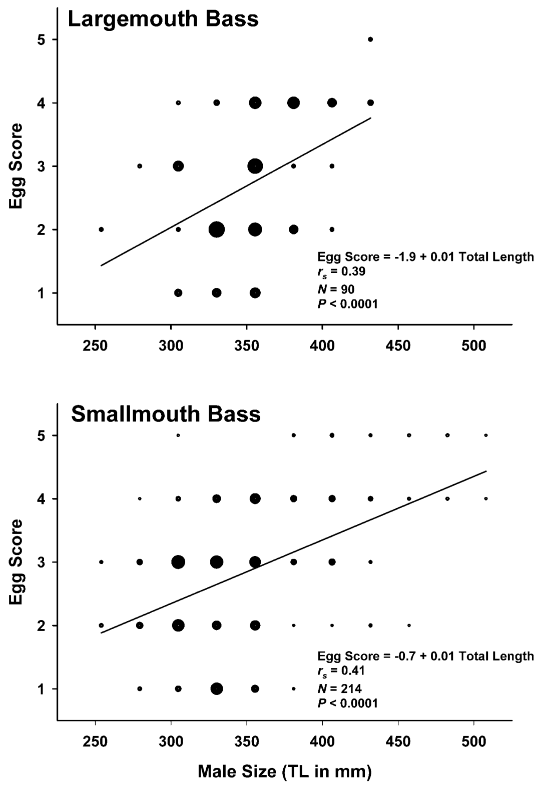

FIGURE 1.—Spearman rank correlation (r_s) examining the relationship between the size of the brood-guarding male (TL in millimeters) and its egg score for largemouth and smallmouth bass. Because similarly sized male bass sometimes had identical egg scores, the size of each point in the figure depicts the number of males represented by that point: smaller points represent fewer nesting males, and larger points represent greater numbers of males. The number of nesting males for each point ranges from 1 (smallest point) to 13 (largest point) for largemouth bass and from 1 (smallest point) to 20 (largest point) for smallmouth bass. To aid in visualization of the relationship between the variables, the regression line has been plotted for each correlation.

sulted in significant increases in brood defense towards the predator model, regardless of male size. Because larger broods equate to greater reproductive success for nesting males, it is not surprising that male largemouth bass and smallmouth bass invested greater amounts of energy (and risk to themselves) in the defense of larger broods (Ridgway 1989; this study).

For both smallmouth and largemouth bass, increases in the size of the nesting male resulted in a significant increase in brood size. This result has been shown in previous studies (Philipp et al. 1997), and may also be influenced by male energy

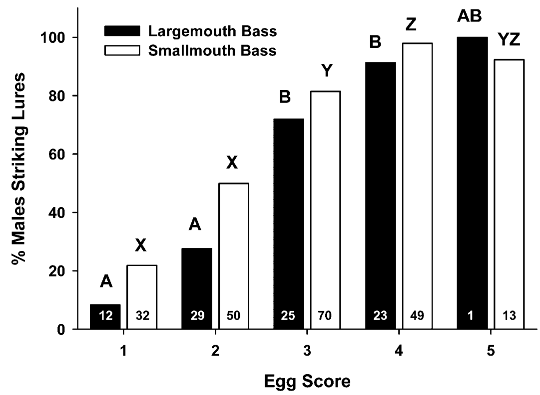

FIGURE 2.—Percentage of nesting male largemouth and smallmouth bass with different egg scores that hit a fishing lure within the allotted six casts. Sample sizes for each group are shown on the individual bars, and different letters above bars denote statistically significant differences within each species (A and B apply to largemouth bass, X, Y, and Z to smallmouth bass). Only one largemouth bass with an egg score of 5 was encountered during the study.

stores (Ridgway and Friesen 1992) or because both large males and large females are reproductively active earlier in the spring than are smaller males and females (Wiegmann et al. 1992). Because these largest males had the largest brood sizes, these males were the ones most likely to be caught by angling as they defended their nests. These large males are not only the most valuable for the

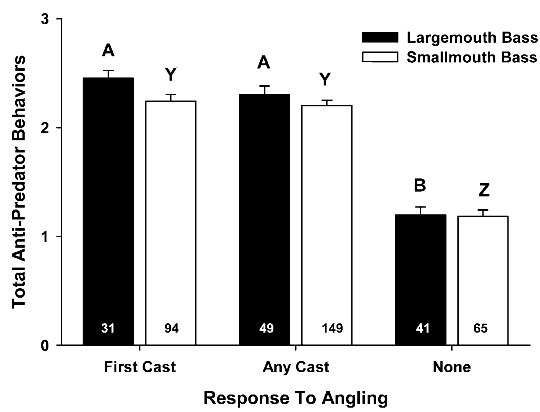

FIGURE 3.—Total antipredator behaviors (TAB score) for nesting male largemouth and smallmouth bass that had differing responses to angling. The term ''first cast'' refers to nesting males that hit the first lure presented (a silver stick bait) on the first cast, the term ''any cast'' refers to males that hit a lure any time during the six casts, and the term ''none'' refers to males that did not hit the lures on any cast. See the caption to Figure 2 for additional details.

fishery, they are also the individuals that are the most willing to invest in the defense and care of their offspring. As such, these males are the ones that have the greatest potential to contribute to annual recruitment.

Our study suggests that largemouth and smallmouth bass were unable to differentiate between potential brood predators and angled lures as both were attacked aggressively and the males that showed aggressive behaviors toward the brood predator were more likely to respond to angling. Although several studies have examined the vulnerability of black bass to angling (Anderson and Heman 1969; Burkett et al. 1986; Lindgren and Willis 1990; Garrett 2002), to our knowledge, only two other studies have quantified the vulnerability of black bass to angling during the nesting period (Latta 1963; Allan and Romero 1975). Latta (1963) had 67% of nesting smallmouth bass respond to angled lures, while only 10% of the nesting largemouth bass tested by Allan and Romero (1975) were caught by anglers. The results of our study agree with those of Latta (1963), but we find the results of Allan and Romero (1975) difficult to understand and see three possible explanations for them. First, the seven experimental anglers in the study by Allan and Romero (1975) were ineffective under the conditions present on the test day. In our study, over half of the nesting males of both species tested were hooked within six casts, and a large proportion hit the lure on the first cast. In addition, during work on other projects, our project personnel routinely catch over 90% of nesting bass targeted when casting attempts are not limited (D. Philipp, unpublished data). Second, the stage of brood development may have differed between the two studies. Previous work has shown that a male's defense of his brood decreases with brood development, and should be lowest as the brood approaches independence (Sargent and Gross 1986; Ridgway 1988). In our study, we angled for males following the deposition of newly spawned eggs when brood defense is typically high, while Allan and Romero (1975) reported observing male bass guarding free-swimming fry during their angling trials, when brood defense by males is typically low. Finally, bass aggression may be related to male energy stores (Hinch and Collins 1991), which may be coupled with stage of brood development and the amount of time that males have been guarding their young. Regardless of these differences, however, our results emphasize the aggression of brood-guarding bass to both brood predators and angling lures.

During this study, the order of lure presentation was fixed for all experimental trials. This method was chosen to standardize lure presentation between different nesting males and to avoid potential difficulties with the interpretation of results that could have arisen with random lure presentation. Future studies, however, should examine the influence that lure type and presentation order has on the response of fish. For example, a random presentation of lures may have elicited a difference in strike responses either between the two test species or within individuals of the same species with different egg scores. Studies of this nature could also involve nonnesting bass and the influence of lure type on the response to angled lures.

Currently, relatively few jurisdictions in North America have regulations designed specifically to protect nesting bass from angling (Quinn 2002). Even in Ontario, where angling for bass is illegal until the last Saturday in June, anglers often do not comply with existing regulations (Kubacki et al. 2002). Illegal angling reduces both individual and population-level reproductive success (Philipp et al. 1997; Suski et al. 2002), which, in turn, may reduce annual recruitment (Svec 2000). One management option that protects nesting bass from angling and improves population-level reproductive success is the use of bass conservation zones. These conservation zones are areas of a water body in which fishing for all species is prohibited during the bass spawning season (Suski et al. 2002). By removing (or at least reducing) the threat of human disturbance through angling, the nest abandonment rates for both smallmouth bass and largemouth bass decreased, thereby increasing population-level reproductive success.

The selective harvest of fishes can influence populations at both a phenotypic and genetic level (Sheridan 1995; Law 2000), often having impacts extending beyond the target species (Tasker et al. 2000; Kaiser and de Groot 2000), and negative population-level changes can occur as a result of the harvest of the largest spawning individuals from a population (Conover and Munch 2002). If anglers target nesting bass, the individual bass caught will not be a random selection; the largest, most aggressive males with the largest broods will be captured preferentially. Over time, catch-and-harvest and even catch-and-release angling for nest-guarding bass are likely to select for smaller, less aggressive males with reduced ability and/or willingness to provide parental care to their offspring.

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