

The Effect of Catch-and-Release Angling on the Parental Care Behavior of Male Smallmouth Bass

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Abstract.—Parental investment theory predicts that parents should adjust the level of care given to offspring relative to brood size and stage of brood development. This variation in parental care results from a trade-off between the reproductive value of the current brood and the reproductive return that the parent can expect to receive from future broods. Our study, carried out in Charleston Lake, Ontario, Canada, examined how handling stress and brood predation associated with catch-and-release angling influenced parental care behaviors and, ultimately, nest abandonment decisions of male smallmouth bass *Micropterus dolomieu*. Individuals were divided into six treatment groups: two different controls ($n = 10$ and 11) and four test groups that were either angled and then released ($n = 11$), had broods reduced manually to simulate predation ($n = 12$), received a combination of angling and brood reduction ($n = 10$), or had their brood size augmented through the manual addition of larvae ($n = 10$). Exposing the fish to a model brood predator revealed that, after catch-and-release events, angled males were less willing or less able to defend their broods than were control fish. In addition, with or without angling, males subject to simulated brood predation were the least aggressive in defending their remaining broods. Moreover, the only treatment groups that showed substantially greater rates of nest abandonment were those that included simulated predation.

Among fish species with paternal defense of offspring, the level of protection provided by a male is influenced by both the quantity and the developmental stage of his brood. Because at any time the number of currently surviving offspring determines the maximum potential fitness for each

male for that particular spawning bout, males should be willing to invest more energy in defending larger broods than smaller ones (Pressley 1981; Carlisle 1985; Sargent and Gross 1986; Ridgway 1989; Coleman and Fischer 1991). In addition, because the reproductive value of offspring increases with the age of the brood, the amount of parental care given by an attending male should increase as his brood grows older (Pressley 1981; Sargent and Gross 1986; Ridgway 1988). As progeny approach independence, however, the care giv-

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en by a male should decrease; further investment may not significantly increase the probability of offspring surviving to adulthood (Sargent and Gross 1986) and may only serve to decrease future reproductive opportunities for that male. Such a decrease in future reproductive opportunities could be realized either in that same year through the prevention of renesting at times when females are still capable of spawning, or in future years through a reduced condition of the male that might prevent future nesting efforts (or even result in premature death). As a result, any event that decreases brood size or a male's energy reserves could potentially influence parental care decisions of the male (i.e., whether or not to continue to provide parental care to his offspring, and, if so, how much care to provide).

Typical of all centrarchids, male smallmouth bass *Micropterus dolomieu* provide sole parental care for developing offspring (Breder 1936). In early spring, when water temperatures reach approximately 15°C (Turner and MacCrimmon 1970), male smallmouth bass excavate shallow, saucer-shaped nests in the gravel substrate of the littoral zone. Once nest construction is complete, females are courted and spawning occurs shortly thereafter. After egg deposition, females leave the area, whereas the male remains to fan the eggs and protect the developing offspring from brood predators (Coble 1975; Ridgway 1988; Ongarato and Snucins 1993; Philipp et al. 1997). The care provided by nesting males can persist for as long as 5 weeks, at which point the young are free-swimming and independent (i.e., they can forage and avoid predators on their own). If a male smallmouth bass leaves his brood unattended, even for a short period, before the offspring develop to the independent free-swimming stage, the offspring are likely to be consumed by predators (Kieffer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997).

Angling for smallmouth bass during the nesting stage can remove a brood-guarding male from his nest, resulting in some cases in nest abandonment (Beeman 1924; Kieffer et al. 1995; Philipp et al. 1997). After catch-and-release angling, however, some parental male bass resume brood defense, guarding offspring until they have reached independence (Philipp et al. 1997). As a result, many anglers target bass during the nesting period under the assumption that catch-and-release angling has no negative effect—an assumption, however, that is incorrect (Kieffer et al. 1995; Philipp et al. 1997; Cooke et al. 2000).

The mechanisms that control the parental care decisions associated with abandonment of broods among male smallmouth bass after catch-and-release angling remain unidentified. Two different components of a catch-and-release angling event may contribute to parental care decisions. First, the actual process of hooking, landing, and releasing a nest-guarding bass, which is already probably somewhat debilitated physiologically as a result of spawning and nest-guarding activities (Cooke et al. 2000), may be quite stressful (Hinch and Collins 1991; Ridgway et al. 1991; Kieffer et al. 1995). This stress alone might be substantial enough to force a male to abandon his brood to ensure his own survival. Second, when males are removed from their brood during the catch-and-release angling event, offspring are exposed to greatly increased predation risk during that period (Beeman 1924; Kieffer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997). As the extent of brood loss increases, the value of that brood to the male decreases. At some amount of brood loss, a male should cease investment in that reproductive bout and conserve resources for future reproductive efforts (Coleman et al. 1985). The purpose of the present study was to assess the relative importance of those two components in influencing parental care decisions among male smallmouth bass exposed to catch-and-release angling.

Methods

Study site and organisms.—Data on nesting smallmouth bass were collected in Charleston Lake, Ontario—a deep (maximum depth = 91.1 m, average depth = 17.4 m) oligotrophic lake in Leeds and Grenville county (44°32'N, 76°01'W). Nesting male bass guarding newly spawned eggs (<24 h old) were located by snorkel survey in late May 1999. Because size and mating success of males affect abandonment rates in smallmouth bass (Philipp et al. 1997), we excluded males that were exceptionally large (>450 mm) or small (<250 mm), as well as males that had uncommonly large or small broods (egg scores of 1 or 5; see below for explanation of egg scores). As an assessment of the baseline parental investment of each male at that time, the snorkeler also determined the rate at which a male fanned his eggs (pectoral fin beats per minute).

To assess individual aggression toward potential brood predators, each nesting male that met body size and mating success criteria was presented with a model of a brood predator. The model was a resin-coated photograph of a bluegill *Lepomis ma-*

crochirus (total length, ~150 mm) mounted on a Plexiglas backing and attached to a 1.5-m-long metal rod (Coleman et al. 1985). For the test, a snorkeler positioned the model in each male's nest and moved it in a way that mimicked egg predation. Four of 68 nesting males fled the area when presented with the bluegill model; these individuals were excluded from the experiment. The remaining 64 males defended their broods vigorously. Those males were marked with individually numbered nest tags, their locations mapped, and the mating success of the male (number of eggs received), scored on a scale ranging from a low of 1 to a high of 5 (Kubacki 1992), was recorded. In addition, the size of the male was estimated visually and recorded. Because many fish were caught by angling during the experiment, visual estimates made by the swimmer and the measured total length of the male could be compared; they were always within 1 cm of each other.

Treatment groups.—Nesting male bass were then placed into one of six treatment groups. Before further testing, male smallmouth bass were assigned to treatment groups so that the distribution of male size, egg scores, and location of nests within the study site were similar across all groups. Because smallmouth bass eggs adhere to the substrate (Pflieger 1966), such that their removal may have resulted in mortality, physical manipulations of the brood and angling activities were performed the day after hatching, when the nests contained egg-sac fry (ESF). The six treatment groups were as follows:

(1) Controls. These fish were not manipulated other than being exposed to behavioral testing (i.e., nest identification and measurement of mating success, determination of fanning rates, and assessment of aggression toward brood predators through model presentations).

(2) Angled. Males were removed from their nests by hook-and-line angling. Bass were hooked within 1 m of their nest, landed quickly, and held for 5 min in a closed cooler containing fresh lake water before being released back into the water within 5 m of their nests. While the male was absent, a swimmer remained at the nest to prevent any brood predation. All males returned to their nests within 3 min after release, at which time brood protection by the swimmer was terminated.

(3) Simulated predation. Males had their broods reduced by 50%. To accomplish this, a diver removed approximately half of the newly hatched fry with a turkey baster and transferred the fry to

a mason jar filled with lake water. The males were present during this procedure and were not angled.

(4) Angled + simulated predation. Males were removed from nests by angling as described for group 2 above, and while these males were in the cooler, a diver reduced their broods by 50% as described for group 3. During this time, the diver prevented any additional brood predation from occurring until the male was released and had returned to its nest. All males returned to their nests within 3 min.

(5) Brood augmentation. Males had their broods doubled in size. While the recipient male was allowed to remain at his nest, a diver added an equal number of fry collected from the simulated predation treatments (groups 3 and 4 above).

(6) Manipulation control. The purpose of this group was to control for disturbance(s) caused by actions of the diver. Males had half of their offspring removed with a turkey baster, transferred to a Mason jar, and then returned to the same nest. The male was allowed to remain at his nest throughout this activity.

The males in this study that were subjected to catch-and-release angling were treated very gently compared with their treatment in typical angling events. In many real-world angling events, brood-guarding males that are removed from their nests are typically away for longer than 5 min, are subject to prolonged air exposures for photographs, and then are released a great distance from their nests. For males subjected to such treatment, previous research has already documented that the incidence of nest abandonment increases substantially (Philipp et al. 1997).

Assessments of aggression toward brood predators.—Before performing any manipulations prescribed by test group assignment, we presented each male in the six treatment groups with the bluegill model to quantify his baseline level of aggression against potential brood predators. In this procedure, the bluegill model was positioned both on the rim of a nest for 30 s and in its center for 30 s, and three aggressive behaviors of the nesting male were quantified (yawn, rush, and hit). A yawn occurred when a male opened his mouth and flared his branchiostegal membranes at the model. 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 (i.e., males could not yawn and rush at the same time) and because all three behaviors were

TABLE 1.—Characteristics of male smallmouth bass by treatment group. Values are means \pm SE, and differences across groups are compared by means of analysis of variance. Measurements were taken prior to manipulations, while males were guarding eggs.

Treatment group and statistic	<i>n</i>	Male size (mm)	Nest depth (m)	Egg score	Fanning rate (beats/min)
Control	10	345 \pm 17	1.2 \pm 0.1	2.9 \pm 0.2	80 \pm 5.3
Angled	11	358 \pm 19	1.2 \pm 0.1	3.0 \pm 0.2	79 \pm 3.4
Simulated predation	12	343 \pm 14	1.2 \pm 0.1	2.9 \pm 0.2	82 \pm 3.5
Angled + predation	10	366 \pm 18	1.2 \pm 0.1	3.3 \pm 0.2	83 \pm 2.6
Brood augmentation	10	353 \pm 15	1.0 \pm 0.2	3.2 \pm 0.2	77 \pm 3.4
Manipulation control	11	349 \pm 13	1.2 \pm 0.1	3.4 \pm 0.3	80 \pm 3.5
<i>P</i>		0.91	0.91	0.53	0.92
<i>F</i>		0.28	0.30	0.84	0.29

exhibited by nesting males, the frequency of all three was summed to determine the total number of antipredator behaviors (TAB score) for that male. The mean TAB score for a treatment group was calculated by summing the TAB scores calculated for males in that group and dividing by the number of males. Immediately after these initial behavioral assessments, males and their broods were manipulated according to the above description for each treatment.

To assess treatment effects, all males were again assessed for their aggression toward the bluegill model predator (with the two-stage presentation scheme used earlier) for 2 d. after the initial behavioral assessments and treatment manipulations. At this stage of nest development, the fry had just begun to develop some skin pigmentation, but were still unable to swim up from the nest substrate. Nests were visited every 2 or 3 d. after this

second aggression assessment to determine presence or absence of the guarding male. Presence/absence observations were continued until the free-swimming fry had metamorphosed from black fry to brown fry (normal juvenile pigmentation) and had become independent of the male's care or until the male had abandoned his nest.

Data analyses.—Statistical tests were performed with JMPIN Version 4.0 (Sall et al. 2000), and the level of significance (α) for all tests was 0.05. Behavioral responses before and after treatments within treatment groups were compared by *t*-tests, and the results of behavioral testing before and after manipulations were compared across treatment groups by using a one-way analysis of variance (ANOVA), followed by a Dunnett's test to compare differences in the treatment groups to the control group (Zar 1999). An ANOVA was also used to compare the means of physical characteristics of the male smallmouth bass in each of the treatment groups, whereas *t*-tests were used to compare the size and egg score of males that abandoned their broods with those males that successfully raised their young (Zar 1999). Regression analysis was used to examine the effect of male size on the TAB score of individual males, and differences in TAB scores across males of different egg scores were compared with an ANOVA (Zar 1999).

Results

Among treatment groups, there were no significant differences in male size, nest depth, egg score, or fanning rates before manipulations (Table 1; ANOVA, all $P > 0.05$). Furthermore, the TAB score before the manipulations was not influenced by either egg score (Figure 1; $n = 64$, ANOVA, $F = 1.44$, $P = 0.24$) or male size (Figure 2; $n = 64$, $F = 0.16$, $P = 0.69$). In addition, before the various manipulations, presenting the bluegill

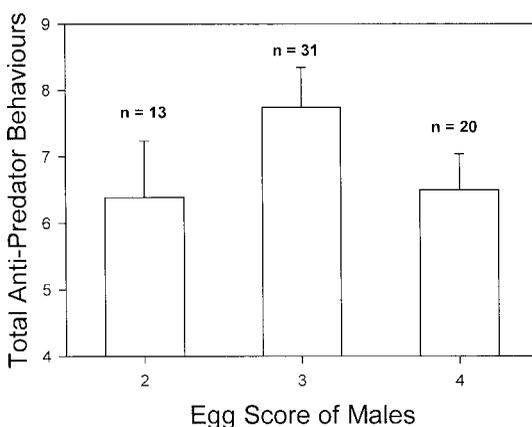


FIGURE 1.—Total antipredator behaviors (TAB score; see text) by males with different levels of mating success (egg scores). Behavioral assessments were conducted before brood manipulations, while males were guarding eggs. Error bars show 1 SE; differences across groups were not significant.

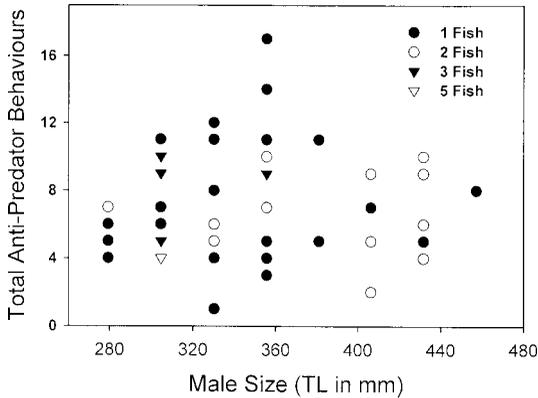


FIGURE 2.—Relationship between total antipredator behaviors (TAB score) and individual male size. Throughout the study, several males were identical in both size and TAB score; the legend details the number represented by each point in the regression. Behavioral measurements were taken before brood manipulations when males were guarding eggs ($n = 64$).

model led to no significant differences in the TAB scores exhibited by males in the various groups (Figure 3; $n = 64$, ANOVA, $F = 1.1$, $P = 0.36$).

After the manipulations, however, the treatment groups varied significantly in their response to the bluegill model (Figure 3; $n = 54$, ANOVA, $F = 9.25$, $P < 0.0001$). Specifically, the TAB scores for the control, manipulation control, and brood augmentation groups increased after manipulation (Figure 3A, B, C), whereas the simulated predation, angled, and angled plus simulated predation groups all showed a decrease in TAB scores after manipulations (Figure 3D, E, F). Increases in TAB score for the manipulation control (Figure 3B; t -test $t = 0.9$, $df = 20$, $P = 0.4$) and brood augmentation groups (Figure 3C; t -test $t = 1.6$, $df = 18$, $P = 0.1$) were not statistically significant, but increases in TAB score for the control group during the experiment were statistically significant (Figure 3A; t -test $t = 2.3$, $df = 18$, $P = 0.04$). Decreases in TAB scores after the treatments were statistically significant for the simulated predation (Figure 3D; t -test $t = 4.4$, $df = 17$, $P = 0.0004$) and the angled plus simulated predation group (Figure 3F; t -test $t = 5.9$, $df = 14$, $P < 0.0001$), but not for the angled group (Figure 3E; t -test $t = 1.0$, $df = 19$, $P = 0.3$). Additionally, the TAB scores exhibited by the simulated predation group and the angled plus simulated predation group after manipulations were significantly lower than the TAB score of the control group (Dunnett's test, $P < 0.05$).

Perhaps most importantly, males subjected to simulated predation (alone and with angling) had greater rates of nest abandonment (67% and 70%, respectively) than males in all other groups. Angling by itself caused only 9% abandonment (Table 2), whereas all of the nesting male smallmouth bass that were not subjected to predation or angling (both of the control groups and the brood augmentation group) were successful at raising their offspring to independence (Table 2).

Within the two treatment groups subjected to simulated predation, males that abandoned their nests were significantly smaller than males that remained to raise their broods (Table 3; $n = 23$, $t = 2.05$, $P = 0.05$). Abandoning males also had lower egg scores, although the difference in egg scores between abandoning males and successful males was not significant (Table 3).

Discussion

Catch-and-release angling for smallmouth bass during the brood-guarding stage has been shown to induce nest abandonment (Philipp et al. 1997). The reasons for this abandonment may be that angled males experience additional physiological stresses (Kieffer et al. 1995; Cooke et al. 2000), brood size has been reduced due to predation while the male is absent from his nest (Beeman 1924; Coleman et al. 1985; Philipp et al. 1997), or a combination of these two factors. The focus of this study was to determine the relative importance of these two components in making parental care decisions among male smallmouth bass after catch-and-release angling (i.e., whether to continue to guard their broods or to abandon in favor of potential future reproductive efforts).

Male smallmouth bass must constantly balance the trade-off between providing parental care to current broods and abandoning those broods in favor of allocating energy toward future reproductive success. Both egg fanning and the protection of their brood from predators are energetically expensive activities for brood-guarding male smallmouth bass (Hinch and Collins 1991; Gillooly and Baylis 1999) and can last for several weeks (Coble 1975). Considering that the males rarely feed during this time (Hinch and Collins 1991), it is not surprising that by the end of the brood-guarding stage males may have decreased lipid content (Mackereth et al. 1999), decreased chances for survival (Sargent 1997), reduced future fecundity (Balshine-Earn 1995), or all of these. Although parental care may serve to increase brood survival, it may concomitantly sac-

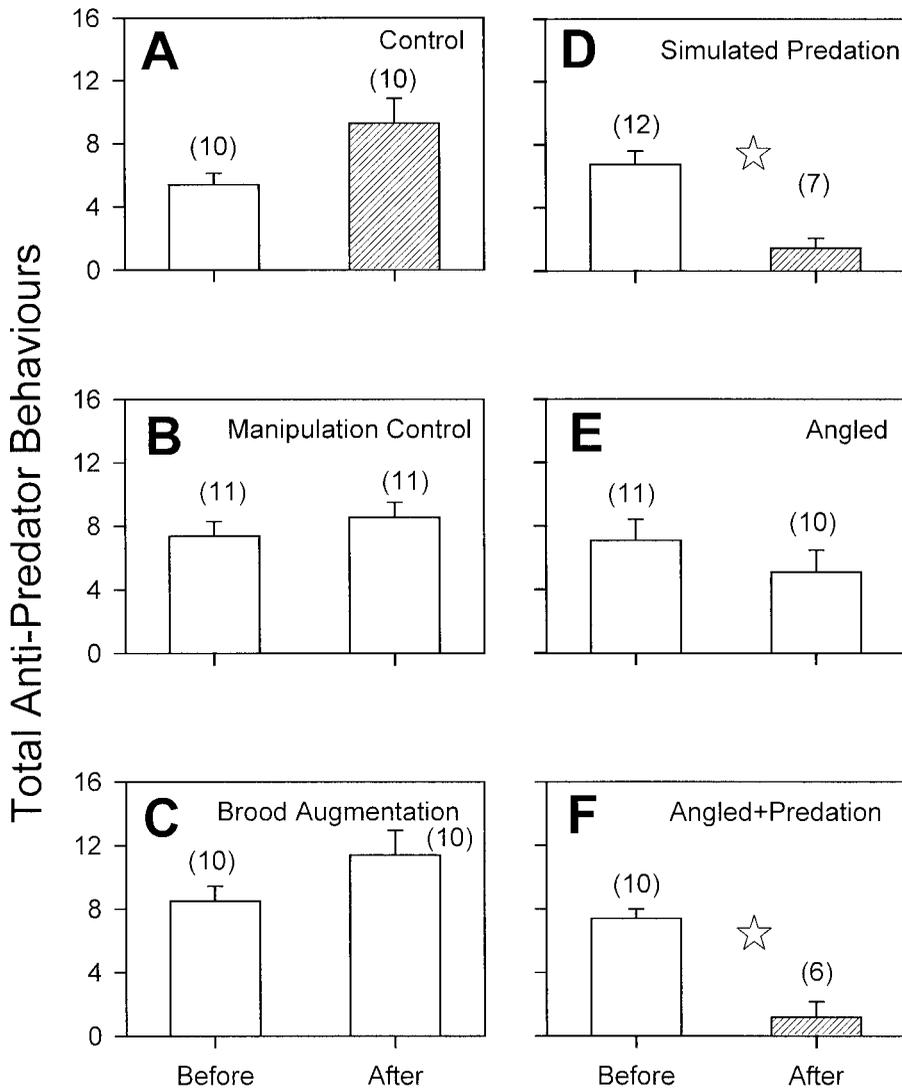


FIGURE 3.—Total antipredator behaviors (TAB score) by nesting males (A) in the control group and (B–F) in the treatment groups before and after manipulations. Stars represent levels of aggression that vary significantly from that of the control group (ANOVA: Dunnett's test, $P < 0.05$), and hatched bars indicate significant differences in TAB score before and after treatments (t -test, $P < 0.05$). Sample sizes for each stage are given in parentheses; error bars show SEs.

TABLE 2.—Occurrence of abandonment for nesting males in each treatment group.

Group	Sample size	Number abandoned	% abandoned
Control	10	0	0
Angled	11	1	9
Simulated predation	12	8	67
Angled + predation	10	7	70
Manipulation control	11	0	0
Brood augmentation	10	0	0

TABLE 3.—Size and egg score of abandoning versus successful males from a combination of the simulated predation and the angled plus simulated predation groups. Mean \pm SE size and egg score for successful males ($n = 7$) and abandoning males ($n = 15$) were compared with t -tests.

Characteristic	Successful males	Abandoning males	P	t
Size (TL [mm])	368 \pm 24	338 \pm 13	0.05	2.05
Egg score	3.3 \pm 0.5	2.9 \pm 0.2	0.12	1.65

rifice future reproductive efforts for the male (Williams 1966; Sargent and Gross 1986). As a result, events that affect the energy status of nest-guarding males will also affect key parental care decisions. Because brood size determines the reproductive potential of each male for that particular spawning bout (Pressley 1981; Carlisle 1985; Sargent and Gross 1986; Ridgway 1989; Coleman and Fischer 1991), which for smallmouth bass is probably the entire spawning season, brood size is a key factor in the decision concerning whether to guard the brood or abandon it in favor of future reproductive opportunities. As a result, any reduction in brood size should affect parental care decisions directly.

In this experiment, a reduction in brood size (through simulated predation) appeared to be the most important factor influencing a nesting male's decision to abandon his nest or not, and this effect was independent of angling. Only the two groups that experienced simulated predation (alone or with angling) showed substantial abandonment rates after treatments (67% and 70%, respectively); angling alone had minimal effect on abandonment (9%). The willingness of nest-guarding males to guard reduced broods (as measured by TAB scores) decreased in the angled group and also decreased significantly in the two groups experiencing simulated predation. This decreased TAB score could be the direct result of physiological disturbances arising from the catch-and-release event (Gustavson et al. 1991; Kieffer et al. 1995) or the indirect result of increased predation on the male's brood during the 2 d between the angling event and the posttreatment aggression assessment with the bluegill model. Furthermore, the brood augmentation group showed increased aggression against the brood predator model (TAB score), suggesting that nesting smallmouth bass constantly assess brood number and consequently defend an enlarged brood more aggressively. A similar conclusion was reached both by Carlisle (1985), who showed that when the brood of a cichlid fish *Aequidens coeruleopunctatus* was augmented, the guarding female defended her offspring more intensely than control females, and by Ridgway (1989), who observed increased nest defense behaviors in smallmouth bass whose broods were augmented through the addition of conspecific offspring.

Among the males in the two groups experiencing simulated predation (the only groups with measurable abandonment), those males that abandoned their broods were significantly smaller than males

that chose to stay and raise their broods to independence. This probably indicates differential expectations for future reproductive opportunities. Larger males are presumably older and therefore have fewer reproductive years left. As a result, they should be willing to stay and defend fewer offspring than smaller (younger) males. In addition, for those fish that were angled, differences in the energy reserves of nesting bass of various sizes could also play a role. Shuter et al. (1980) proposed that larger smallmouth bass have greater energy reserves after winter than smaller bass. Previous studies have also shown that the relative standard metabolic rate (Brett 1965; Brett and Groves 1979) and the relative cost of swimming (Schmidt-Nielsen 1972) are greater for smaller fish. As a result, after a disturbance such as angling, small male bass may expend proportionately more of their energy stores than large males and may be quicker to abandon their broods in favor of survival for future reproduction.

The results of this study have important implications for smallmouth bass management not only in Ontario but also throughout the species' range; extended male parental care is ubiquitous in all populations. Further, because male parental care is a life history trait common to all centrarchid species (Breder 1936), we deem it reasonable to assume that evolutionary mechanisms controlling parental care decisions are similar throughout the genus *Micropterus*. Two facts, when coupled, support this assumption. First, smallmouth and largemouth bass both demonstrate similar negative responses to catch-and-release angling (Philipp et al. 1997). Second, these two species are the most distantly related of the genus *Micropterus*, each residing within a different phylogenetic lineage within the genus (Kassler et al. 2002). To assume that all of the intermediate forms (species) share these properties is more parsimonious than inferring that two separate evolutionary events occurred. As a result, conclusions based on these experiments with smallmouth bass should be directly applicable to all black bass species.

Currently, many regions of North America do not offer any regulatory protection to black bass during the nest-guarding period (Quinn 1999); the males are thus subject to both catch-and-harvest angling and catch-and-release angling. If a male bass is removed from his nest through catch-and-harvest angling, the brood will probably be consumed by predators and will not survive (Beeman 1924; Kelley 1968, Coble 1975; Neves 1975; Philipp et al. 1997), thereby eliminating that male's

reproductive output for that and all future spawning seasons. If a male is removed from his nest temporarily, such as in catch-and-release angling, his brood is left defenseless for a certain period, and predators may consume a portion of the offspring. If the brood size should be substantially reduced, we have shown in the current study that this will increase the likelihood of abandonment by the male, again resulting in the total loss of reproductive success for that particular spawning bout. Other authors have raised concerns about the sustainability of bass populations subject to angling during the brood-guarding stage (Kieffer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997), which may be particularly important if recruitment in bass is influenced by population-level reproductive success (Svec 2000) or spawner abundance (Myers and Barrowman 1996).

By creating regulations that protect bass from any form of angling (either intentional or accidental) during the highly vulnerable nest-guarding stage, abandonment rates should be reduced (Philipp et al. 1997; Ridgway and Shuter 1997). This protection could be accomplished through regulations that restrict angling through seasonal closures (Quinn 1999) or through the use of no-fishing sanctuaries (Suski et al. 2002). Both of these regulatory strategies have the potential to protect nesting bass, but the realization of that potential depends on several factors. For closed seasons, two important issues are involved. First, the closed season must, in fact, span the entire period of spawning through the end of parental care, a period that in Ontario may last 6 to 7 weeks and may start at different times each year, depending on environmental factors. Second, if angling for other species is allowed during the closed bass season, enforcement of prohibited angling for nesting bass becomes very difficult. For no-fishing sanctuaries, the key to success lies in protecting enough good spawning habitat to make a difference and enforcing that protection through prohibition. This enforcement may involve restricting angling in 20–30% of the littoral zone of a lake. Designating as a sanctuary 1–2% of a lake's littoral zone (especially if that consists of shallow, swampy areas in which bass do not spawn) will provide little benefit. Of course, both of these restrictive actions will decrease angling opportunities (either temporally or spatially), but that short-term sacrifice may be key to maintaining, or even improving, our bass populations in the long term.

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