When and why do smallmouth bass abandon their broods? The effects of brood and parental characteristics

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Abstract
Variation in brood abandonment was explored by conducting partial brood removals from smallmouth bass, Micropterus dolomieu Lacepède, nests in two north temperate lakes. In both lakes, percent of the brood removed had no effect on nest failure rates. Nest failure prior to offspring swim-up was more common, but unrelated to brood size after removal, in the lake with higher post-spawning mortality and lower growth and fecundity. Brood size after removal was negatively related to nest failure in the lake with high survival, growth and fecundity. Nests guarded by young males failed more frequently than those of old males, and young broods failed more frequently than old broods. Dynamic programming and logistic regression models developed to predict nest fate worked better for the lake with selective pressures that theoretically favoured abandonment (e.g. high post-spawning mortality). Both models identified male age and brood age as important factors in predicting nest fates. Because nest success is related to the age of the parent, this could have consequences for overall nest success for populations with different demographics.

KEYWORDS: brood abandonment, brood predation, Micropterus dolomieu, nest success, parental care.

Introduction
Parental care can be energetically costly for a parent but is required for many species or the offspring will perish. Providing care can reduce parental survival, growth and breeding interval, thus reducing future breeding attempts and their expected future fitness (Sabat 1994; Balshine-Earn 1995; Székely & Cuthill 2000). Therefore, species that provide parental care face a trade-off between current and future fitness (Williams 1966; Trivers 1972). If the benefits to future fitness by abandoning the current brood exceed the expected return of continuing to provide care, abandonment would be the optimal behaviour. Although individuals might not be continuously assessing the costs and benefits of guarding or abandoning their brood, natural selection should favour those that choose the behaviour that increases lifetime fitness. In this theoretical context, reproductive effort, including providing care, should be predictable and probably depends on factors such as adult survival and fecundity, as well as juvenile survival and growth (Clutton-Brock 1991; Stearns 1992; Hutchings 1993). For species that care for their offspring, current brood size is an important factor determining the amount of care provided (Armstrong & Robertson 1988).

There is considerable variation in the amount of parental care provided among different species. Brood abandonment following changes to the current brood varies. The most common pattern in birds has been an increase in brood abandonment with a reduction in clutch size (Armstrong & Robertson 1988; Székely & Cuthill 2000), but there are exceptions. Nests parasitised (i.e. loss of at least some of the original brood) by brown-headed cowbirds, Molothrus ater Boddaert, have been reported to have both higher abandonment rates (Clotfelter & Yasukawa 1999) and little change in abandonment (Whitehead et al. 2000). Eurasian kestrel, Falco tinnunculus L., parental effort has been reported to remain relatively constant across manipulated brood sizes (Tolonen & Korpimäki 1996) and to be positively related to brood size (Dijkstra et al.)
In addition, red-backed salamanders, *Plethodon cinereus* Green, also tend to abandon small broods more than large broods (Yurewicz & Wilbur 2004). Fishes also demonstrate increased abandonment or filial cannibalism of small broods (Petersen 1990; Suski et al. 2003; Hanson et al. 2007). Finally, cuckoldry (extra-pair fertilisations) often result in cannibalism or abandonment in fishes and birds (Mauk et al. 1999; Neff 2003).

Although one might think parental care is predictable, it is apparent that there is considerable variability that may be caused by environmental or demographic differences among populations. The goal of this research was to assess variability in parental care in a nest-guarding fish, the smallmouth bass, *Micropterus dolomieu* Lacepède, in lakes with different selective pressures. Male smallmouth bass provide sole parental care for their offspring, sometimes for more than 1 month (Ridgway 1988). As with other organisms, this care is costly, resulting in increased mortality (Ridgway 1986; Dunlop et al. 2005) and a loss of energetic content (Gillooly & Baylis 1999; Mackereth et al. 1999; Steinhart et al. 2005b), the latter of which may reduce the number of eggs a male receives in the future (Wiegmann et al. 1992; Mackereth et al. 1999). Angling of nest-guarding males can substantially increase brood abandonment in some systems (Suski et al. 2003; Hanson et al. 2007), but in other lakes the effects are minor (Steinhart et al. 2005a).

The specific objectives of this study were to: (1) assess if experimentally reduced broods were more likely to fail than unmanipulated broods; (2) explore how male age, and brood age and size affected nest failures; and (3) evaluate two modelling techniques for predicting nest abandonment. From parental care theory, it was hypothesised that nest failure (i.e. abandonment) would increase as the percent brood removed increased and as male age, brood size and brood age decreased. If brood abandonment is predictable, then it may be possible to forecast the potential effects of perturbations, such as angling, that affect parental behaviour and even predict resulting impacts on offspring production or recruitment success.

**Methods**

**Field surveys**

Smallmouth bass nests were located via snorkelling surveys in known spawning areas in Lakes Opeongo and Provoking, Algonquin Provincial Park, Ontario, Canada. Lake Opeongo (58.6 km²) contains various fishes, including yellow perch, *Perca flavescens* (Mitchill), pumpkinseed, *Lepomis gibbosus* (L.), lake trout, *Salvelinus namaycush* (Walbaum), several cor- egonids and many cyprinids (Martin & Fry 1973). Provoking Lake is only 11 km² and supports only smallmouth bass, splake, *S. namaycush* × *Salvelinus fontinalis* (Mitchill), and yellow perch. Both lakes have populations of smallmouth bass that were introduced in the early 1900s. The smallmouth bass populations are quite different, however, with the Provoking Lake population characterised by higher densities, slower growth rates, earlier maturation and higher post-spawning mortality than smallmouth bass in Lake Opeongo (Dunlop et al. 2005).

Snorkel surveys were conducted during 31 May to 12 June 2007 in Opeongo and 3 June to 29 June 2008 in Opeongo and Provoking to locate smallmouth bass nests and monitor their success following experimental brood removals. Different stretches of shoreline were sampled each year in Lake Opeongo to avoid any resampling or cumulative effects of the brood remo- vals. Nests were marked with numbered rocks to ensure proper identification on subsequent visits that occurred typically every 2 days (range 1–4 days). Male presence or absence and offspring developmental stage were recorded on each visit. Developmental stages were defined as unhatched embryos (eggs), hatched embryos (clear fry or pigmented fry), larvae (swim-up fry) or juveniles (green fry still associated with a nest and guarding male). Nests containing free-swimming larvae were deemed successful while nests that did not reach the larval stage were considered failures. Because angling for smallmouth bass was not allowed during the survey period and there are few predators of adult smallmouth bass in the lakes, nest failures were considered abandoned nests, although unobserved sources of adult or offspring mortality could have led to some nest failures.

Brood-removal treatments were systematically as- signed to nests starting with 0% brood removal and continuing to 25%, 50%, or 75% brood removal. However, because treatment assignments varied in space (i.e. where nests were found or treated on a given day) and time (i.e. the day nests were found or treated), the treatment assignments were essentially random. Some newly discovered nests had treatment assignments reserved for a later date to allow for manipulation of older broods. For all treatments, nest-guarding smallmouth bass were removed from their nests via angling with a single-hook jig. Total length (TL, mm) and wet weight (nearest 5 g) were measured, scale samples were collected to estimate
age and then the fish was released. This procedure was performed as quickly as possible (typically < 30 s) to reduce stress and air exposure to the fish. All males returned to their nest, at least temporarily, within 10 min after release.

Brood removals and information on the brood characteristics were collected immediately following angling of the male. A 0.5-m² PVC frame, divided into eighths with string, was placed over the brood such that approximately equal numbers of offspring were in each eighth of the frame (based on visual estimation of the area and density of offspring in each section). A turkey baster was used to remove offspring from adjacent sections corresponding to treatment level (e.g. two of the eight sections to achieve 25% brood removal). All collected offspring were transferred to an individually labelled jar filled with 70% ethanol.

Brood ages were known for nests where spawning was observed or when the nest was sampled on consecutive days immediately before and after egg deposition. If the exact spawning date was unknown, brood age was determined by comparing brood development with nests of known ages. Age of the guarding male was determined by two readers independently viewing scale impressions on acetate slides. When the age estimates were not in agreement, the slides were viewed in concert until there was consensus on the age. Total brood size was estimated from counts of offspring removed from broods (e.g. if 25% of the brood was removed, the total count was multiplied by 100/25 for an estimate of the brood size). For broods from which no offspring were removed (0% treatment), brood size was estimated with multiple linear regressions of male age and spawning date vs estimated brood size from brood removals in 2007 and 2008 [Opeongo: brood size = 23.72 (TL) + 79.10 (spawning date) – 17 835, $r^2 = 0.20$; Provoking: brood size = 0.018 (TL) – 2.06 (spawning date) + 591.70, $r^2 = 0.27$].

Male age, brood age and brood size were compared among treatments with one-way ANOVAs to test for differences among treatment groups. Logistic regressions were used to test if treatment (percent of brood removed) or year (for Lake Opeongo) was related to percent nest failure. To determine if brood size after treatment, age of brood at treatment or male length and age differed between successful and failed nests, one-tailed $t$-tests were used because there were specific directional hypotheses. All analyses were performed using Intercooled STATA 9.2 (Stata Corporation, College Station, TX, USA), with $\alpha = 0.05$ for all tests.

**Predictive modelling**

Two different modelling techniques were used to predict nest failure. A dynamic programming (DP) model, described in Steinhart et al. (2008), was used to predict brood abandonment by nest-guarding smallmouth bass based on age of the guarding male, number of offspring remaining in the current brood and days of care provided. DP models are backward-iterative models that find the optimal solution given a set of state variables (e.g. male age, brood size) and probabilistic conditions (e.g. probability of nest success). Several logistic regression models were developed to predict nest abandonment and were compared using Akaike’s Information Criterion to choose the most parsimonious model (Burnham & Anderson 2002). For each model, the observed results were compared with the predicted results to evaluate the accuracy of the models for predicting nest success and failure.

The DP model predicted at what brood size a smallmouth bass would abandon its offspring. The model assumed males behaved to maximise their lifetime fitness; thus, the male behaviour predicted by the model, either guarding or abandoning, was that which produced the largest expected lifetime offspring production. Expected future fitness, measured as the predicted number of future offspring given the male’s behaviour, was calculated based on the male’s age, size, growth potential, and the size and age of the current brood, as well as several empirically measured probabilities. Daily probability of nest failure because of environmental factors (0.015 day$^{-1}$; Steinhart et al. 2008) was assumed constant in both lakes. The daily probability of being caught by an angler (0.05) and the probably of being released when captured (0.99) were assigned and assumed equal for both lakes because the two lakes experience little angling for smallmouth bass during the spawning season when angling for smallmouth bass is prohibited. Daily offspring survival was estimated at 0.9 day$^{-1}$ for embryos and 0.92 day$^{-1}$ for larvae in Lake Opeongo (Steinhart et al. 2008) and assumed to be the same in Provoking Lake because it has a similarly low predator burden. Field data collected in this study were used to update length-at-age and length–fecundity relationships for Lake Opeongo and to generate these relationships for Provoking Lake (Table 1; and see Steinhart et al. 2008). Adult annual survival rates were calculated for Lake Opeongo based on the observed age structure (Mark Riddaway, Ontario Ministry of Natural Resources, unpublished data; Table 1). Insufficient data were available to estimate annual survival for Provoking Lake, so adult survival rates were assumed to be the
was used to evaluate competing models. AICc scores identified the most parsimonious model(s), those with the best combination of the best fit and the fewest parameters. Models were ranked based on the model likelihoods. The ratio of likelihoods, or evidence ratio, shows how much more likely one model is compared with another. Normalised Akaike model weights, often treated as the probability of a model being the best-supported model among all candidates, were calculated. Individual variables were ranked by summing all Akaike weights for models containing that particular variable (Burnham & Anderson 2002).

### Results

#### Field surveys

A total of 138 nests, 105 in Lake Opeongo and 33 in Provoking Lake, were monitored until they were deemed successful or failures (Table 2). In general, guarding male smallmouth bass were older, larger and had larger broods in Lake Opeongo than in Provoking Lake. However, within each lake male age, brood age at treatment or estimated brood size before treatment did not differ among brood-removal treatments (Table 2).

Nest failure rates generally were lower in Lake Opeongo (22 of 105 nests, 21% failed; Fig. 1) than in Provoking Lake (13 of 33 nests, 39% failed). Neither year (Wald’s statistic = 2.68, \( P = 0.10 \)) , treatment level (Wald’s statistic = 0.86, \( P = 0.35 \)) nor the model with treatment and year (Likelihood ratio \( \chi^2 = 3.63, P = 0.16 \)) affected nest failure rate in Lake Opeongo. In Provoking Lake, nest failure rate was not affected by treatment (Likelihood ratio \( \chi^2 = 0.08, P = 0.77 \)). Although the brood-removal treatment had no effect on nest fate, brood size after treatment was significantly lower for failed nests (1554 ± 262 offspring; mean ± SE) than successful nests (2150 ± 229) in Opeongo (\( t = 1.71, \text{ d.f.} = 57, P = 0.046; \text{ Fig. 2a} \)). In Provoking, however, there was no difference in brood size after treatment between successful (837 ± 118 offspring) and failed (663 ± 141) nests (\( t = 0.94, \text{ d.f.} = 31, P = 0.18 \)).

Nest fate was related to male length, age and brood age in both lakes. In Lake Opeongo, failed nests were guarded by males that were on average 34-mm shorter (\( t = 2.76, \text{ d.f.} = 48, P = 0.004; \text{ Fig. 2b} \)) and 1.3-year younger (\( t = 3.66, \text{ d.f.} = 66, P < 0.001; \text{ Fig. 2c} \)) than males with successful broods. Failed nests were 1.9-day younger on the day of brood removal than age of successful nests in Lake Opeongo (\( t = 4.37, \text{ d.f.} = 73, P < 0.001; \text{ Fig. 2d} \)). Nests that failed in Provoking Lake also were guarded by smaller (274 vs 284-mm) males, and these males were 1.3-year younger (\( t = 4.37, \text{ d.f.} = 73, P < 0.001; \text{ Fig. 2d} \)).

Table 1. Age-dependent parameter values for male smallmouth bass included in the stochastic dynamic programming model. Smallmouth bass in Lakes Opeongo and Provoking had different total length at age (TL, in mm), initial brood size (B), adult annual survival rate (ASR) and cost of parental care (AASR; daily reduction in ASR when guarding). See the Methods for explanations of parameters values.

<table>
<thead>
<tr>
<th>Age</th>
<th>Lake Opeongo</th>
<th>Provoking Lake</th>
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<tbody>
<tr>
<td></td>
<td>TL</td>
<td>B</td>
</tr>
<tr>
<td>4</td>
<td>259</td>
<td>940</td>
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<tr>
<td>5</td>
<td>285</td>
<td>1474</td>
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<td>6</td>
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<td>9</td>
<td>406</td>
<td>3963</td>
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<tr>
<td>10</td>
<td>428</td>
<td>4415</td>
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<td>11</td>
<td>448</td>
<td>4827</td>
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<td>12</td>
<td>466</td>
<td>5197</td>
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<td>13</td>
<td>482</td>
<td>5526</td>
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<tr>
<td>14</td>
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<td>5835</td>
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<tr>
<td>15</td>
<td>512</td>
<td>6143</td>
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<td>16+</td>
<td>512</td>
<td>6410</td>
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306 mm; $t = 2.48$, d.f. $= 31$, $P = 0.009$; Fig. 2b) and younger (6.1 vs 7.4 years; $t = 2.32$, d.f. $= 31$, $P = 0.01$; Fig. 2c) males than successful nests. Failed nests in Provoking Lake also contained younger offspring when brood removal occurred than successful nests (3.5 vs 4.9 days; $t = 2.46$, d.f. $= 31$, $P = 0.01$; Fig. 2d).

### Predictive modelling

The most parsimonious logistic regression model in both lakes included only male age and brood age at treatment (Table 3). In both lakes, the best-supported models were more than twice as likely to be the best models as the second-most parsimonious models. For Lake Opeongo, the model containing male age and brood age at treatment was a significant predictor of nest failure (Likelihood ratio $\chi^2 = 16.42$, $P < 0.001$). The second-best model in Lake Opeongo contained both brood age and brood remaining after treatment, and the third-best model contained only brood age. In Provoking Lake, the model containing brood age and male age was also the best model and a significant predictor of nest fate (Likelihood ratio $\chi^2 = 12.22$, $P = 0.002$); the second-best model contained only brood age, and the third-best-supported model contained only male age.

Additional support for the importance of male age and brood age at treatment was seen after summing Akaike weights for each model containing a particular variable. Models containing brood age at treatment had the greatest sum (0.96 for Opeongo and 0.79 for Provoking), and models with male age had the second highest (Opeongo $= 0.65$, Provoking $= 0.72$). Models containing brood remaining (Opeongo $= 0.32$, Provoking $= 0.18$) or percent of brood removed (Opeongo $= 0.20$, Provoking $= 0.12$) had much lower summed Akaike weights. Male age and brood age had
negative coefficients indicating that older males and older broods were more likely to be successful than young males or young broods. Although the results suggest that the brood remaining after treatment and percent of brood removed were not strong predictors of nest fate, the coefficients suggested a trend for larger broods and nests with a lower percent of offspring removed to be more successful.

Despite the relative statistical superiority of the best-fitting logistic models, the models had mixed results for predicting brood failure (Table 4). The most parsimonious logistic model correctly predicted 75% of nest...
fates in Lake Opeongo and 79% of fates in Provoking. Predicting nest failures was problematic in Lake Opeongo: no failed nests were classified as such. The best-supported logistic model performed better in Provoking Lake, correctly predicting 71% of nest failures. The DP model correctly classified 74% of all nest fates in Lake Opeongo, but only 14% of failed nests were predicted to be abandoned. For Provoking Lake, the DP model correctly classified 61% of the nest fates and 38% of the nests that failed.

Discussion

Brood size and percent brood reduction had little effect on nest failure in this study. Specifically, percent of brood removed did not significantly affect nest failure in either study lake, and brood size affected nest failure only in Lake Opeongo but was not an important variable in the logistic regressions for either lake. These results may have been influenced by the great variability in the number of eggs received by male smallmouth bass. Multiple linear regressions using male length and spawning date to predict brood size had low coefficients of determination (<0.3 for both lakes), so the predicted brood sizes for the 0% brood reduction treatment may have been inaccurate. However, for the nests that received brood reductions (105 out of 138 nests in this study), the estimated brood sizes were probably more accurate because there was a direct count of 25–75% of the offspring. It is also possible that males may not be able to assess the number of offspring in their broods, but this is not likely given that male smallmouth bass have been shown to adjust their nest-defence behaviour according to brood size (Ridgway 1989).

Male age and brood age were found to differ between failed and successful nests and were identified as the most important variables in the best-fitting logistic models. This supports the idea that parental investment is tied to factors other than number of offspring (Tolonen & Korpimäki 1996). Indeed, an analysis of 20 years of nesting data from Lake Opeongo revealed that male body size, which was strongly related to male age, was an important predictor of nest success, especially later in the parental care period when the energetic costs of care may lead small males to abandon (Suski & Ridgway 2007). In addition, Steinhart et al. (2008) provided evidence from simulation models that annual adult survival was the most important factor affecting brood abandonment of nesting smallmouth bass. Functionally, adult survival and male age may have a similar effect on parental behaviour because they both relate to the expected number of future breeding attempts: old males or males with low annual survival have fewer expected future breeding attempts and, therefore, should be more likely to guard their current brood. A growing body of literature suggests that size-selective fishing mortality affects many life-history and behavioural traits, sometimes in only a few generations (e.g. Olsen et al. 2004; Walsh et al. 2006). For fish that provide care when faced with high adult mortality (i.e. few breeding attempts), the most successful fish would likely be those that guard their broods even when the fitness value of the offspring is relatively low. Conversely, fish that were prone to abandoning would be less likely to produce a successful brood during their few reproductive attempts and their genotype would be less likely to persist. Alternatively, if high annual mortality reduces smallmouth bass density and increases their growth rates, individuals may be able to allocate more time and energy to parental care, again resulting in an increased willingness to guard small broods.

Because annual survival, growth and cost of care vary among systems (Dunlop et al. 2005; Steinhart et al. 2005b; Cooke et al. 2008), it is not unexpected that abandonment behaviour should vary between populations. Overall, nest failures were more common in Provoking than in Opeongo in this study. This observation may have been because of low growth and high post-spawning mortality (which decreases overall annual survival) in Provoking compared to Opeongo (Dunlop et al. 2005). Because providing care is known to decrease growth and survival (Sabat 1994; Balshine-Earn 1995; Székely & Cuthill 2000), fish in lakes with low growth and survival not only may be more prone to abandon because of conditions in the lake, but also because the energetic cost of providing care may be more significant or cannot be recuperated during the non-nesting season (Steinhart et al. 2005b). As a result,

### Table 4. Classification matrix for the logistic regression models and dynamic programming (DP) models for actual smallmouth bass nest fates (failed or successful) and model predicted fates. Bold numbers indicate correct classifications.

<table>
<thead>
<tr>
<th></th>
<th>Opeongo Failed</th>
<th>Opeongo Successful</th>
<th>Provoking Failed</th>
<th>Provoking Successful</th>
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<tbody>
<tr>
<td>Logistic model Predicted failure</td>
<td>0</td>
<td>4</td>
<td>10</td>
<td>4</td>
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<tr>
<td>Logistic model Predicted success</td>
<td>22</td>
<td>79</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>DP model Predicted failure</td>
<td>3</td>
<td>8</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>DP model Predicted success</td>
<td>19</td>
<td>75</td>
<td>8</td>
<td>15</td>
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of brood size not being important in determining nest failure in Provoking, while brood age and male age were, supports that notion that population demographics may be important to parental care behaviour. In systems where brood size is not an important factor in nest failure, brood predation should not lead to increased nest failures, as was demonstrated in Lake Erie (Steinhart et al. 2005a).

It is unclear why both modelling techniques were better at predicting abandonment in Provoking Lake than in Lake Opeongo. One possibility is that the demographics in Provoking, which were characterised by slow growth, high post-spawning mortality and low fecundity, select for fish that have a better-defined and higher brood-size abandonment threshold because providing care more strongly affects future fitness via poor growth and survival in Provoking Lake. In the more benign Lake Opeongo, higher expected fitness and lower consequences for providing care (i.e. costs are ameliorated by better growth during the non-nesting season) may allow males to be more flexible in providing care. An alternative hypothesis is that some males may have abandoned in Lake Opeongo because of storms that created waves and may have cause rapid temperature changes as a result of seiches (MacLean et al. 1981). Such storm events would likely be more common in larger Lake Opeongo than in Provoking and would not be predicted in the models. Finally, several DP model parameter values were assumed, especially for Provoking Lake fish, which may have led to poor prediction of nest abandonment. The variables deemed most important to the DP model by Steinhart et al. (2008) were adult annual survival and cost of providing care. For this study, it was assumed that the base annual survival rates were identical in both lakes. If poor growth rates, or some other factor, in Provoking Lake led to lower annual survival than what was used in the DP simulation, it would lead to an underestimation of brood abandonment (i.e. high adult survival in the model would favour nest abandonment). Despite this shortcoming, the results suggest that the model worked better in Provoking Lake than in Lake Opeongo, so the assumed base survival rates might not have been as important as the adjustments to annual survival based on duration of parental care which were based on known values (Dunlop et al. 2005). Therefore, although not all model parameters were explicitly measured in the field, the results still point towards a stronger effect of brood age, male age and adult annual survival (including the effects of parental care on adult survival) on nest success than the effects of brood size and brood reduction.

Other studies have examined the effect of brood removals on smallmouth bass nest success with variable conclusions (Fig. 3). In Lake Erie, Ohio, where nest predators [i.e. round gobies, Neogobius melanostomus (Pallas)] are extremely abundant, brood predation during catch-and-release angling typically resulted in a loss of 25–50% of the offspring in a nest (Steinhart et al. 2004a), but this predation resulted in no difference in nest success from control nests (Steinhart et al. 2005a). Smallmouth bass in Lake Erie have high growth rates compared with many other populations (Doan 1940; Steinhart et al. 2004b), likely ameliorating the cost of providing care (Steinhart et al. 2005b). Relatively high angling pressure should increase mortality and lead to a shorter expected life span in Lake Erie than in lakes in this study and, possibly, a ‘grow and reproduce quickly’ life history (Shuter et al. 2005). These factors should favour a guard strategy even at small brood sizes. In limited experimental brood manipulations (25%–75% of offspring removed) in Lake Erie, 10 of 11 males continued to guard their broods after brood reduction, at least until a storm occurred (mean 6 days, range 0–19 days; Steinhart et al. 2005a).

By contrast, removing 50% of broods in Charleston Lake, Ontario, led to a 61% increase in abandonment...
compared with an angled control (Suski et al. 2003). In the Suski et al. (2003) study, manipulated nests were limited to average-sized broods guarded by average-sized males (presumably these were not the youngest individuals to spawn). Because the current study suggests that young males are more prone to abandonment, the brood removals in Charleston Lake may have been biased towards males that were less likely to abandon, which means that across the whole population the increase in nest abandonment could have been higher. Furthermore, only nests older than 4 days were manipulated by Suski et al. (2003), again biasing the sample towards broods that, based on the results of the current study, may have been less likely to be abandoned. Another manipulation study removed 90% of the brood from smallmouth bass nests in Devil and Wolfe Lakes, Ontario (Hanson et al. 2007). For the Hanson et al. (2007) study, there was no male size-selection and only young nests (<4 days old) were manipulated, so any biases could have favoured abandonment because of the young brood ages. Still, the 67% increase in nest abandonment was much greater than observed in lakes Opeongo and Provoking. Data on growth rates and adult survival were not presented in the above studies, but certainly there was some factor that caused males in these lakes to be less willing to guard experimentally reduced broods than observed in lakes Opeongo, Provoking or Erie. Given the variable effects of brood reduction on smallmouth bass nest success, it is advisable that future experiments be conducted in a range of systems that incorporate variability in key parameters (e.g. annual survival, growth rate, cost of parental care) and that brood manipulations are conducted across a range of brood and male ages.

Providing parental care involves many factors besides only the expected fitness return from the current brood (i.e. brood size). Therefore, understanding how other factors affect care decisions is essential for improving prediction, management and conservation of smallmouth bass, and possibly other species, that provide parental care. It remains to be determined if nest success or number of juveniles produced is linked to adult recruitment in smallmouth bass (Ridgway & Philipp 2002). Until this link is better understood, the conservative approach is to assume that there is a relationship between juvenile production and adult abundance, at least at low levels of offspring produced. Thus, the degree to which angling or brood predation affects nest abandonment varies across systems so the risk of brood abandonment should be considered when setting regulations. The results of this research suggest that certain populations may be more prone to abandonment and, therefore, might benefit from more protective regulations. For example, establishing no-take zones or minimising disturbances may produce a greater increase in offspring production in systems where males are more likely to abandon (e.g. lakes with high mortality, low growth or fecundity, or high parental care cost) than in systems where males tend to guard. Therefore, fisheries managers may be able to improve their ability to manage populations when they can predict the effects of angling on the nest success based on relatively simple-to-collect demographic parameters (e.g. annual survival, age structure). While the model simulations did not do a good job in predicting abandonment, characteristics of the nest and the guarding male did vary among successful and failed nests. Future efforts can refine these models and consider other variables to improve the ability to predict brood abandonment for smallmouth bass and other nest-guarding fishes.

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