

Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish

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ABSTRACT

Background: Parental care generally increases offspring survival but, for the parent, providing care can reduce adult growth and survival. Therefore, a trade-off exists between investments in current or future reproduction, and populations with different demographics and selective pressures may have different thresholds for when and how much care they provide.

Question: How variable are different populations of smallmouth bass *Micropterus dolomieu* in their willingness to provide care for small broods? What factors are most important in determining optimal brood abandonment thresholds?

Methods: We used dynamic programming to explore how adult and juvenile survival, brood predation, probability of nest success, angling pressure, and parental care costs affected brood abandonment thresholds.

Results: Adult annual survival was the most significant factor in determining optimal parental care decisions. Abandonment was less likely when adult annual survival and offspring daily survival were low than when survival was high. High parental care costs led males to abandon larger broods. Factors varying with parental age (e.g. adult survival or cost of providing care) were more important in determining abandonment behaviour than age-independent variables (e.g. offspring survival or probability of nest success) in part because of the larger brood sizes for older, larger males. Increasing angling pressure, storms or nest predators increased abandonment thresholds, but to differing degrees.

Keywords: dynamic programming, expected fitness, nest abandonment, nest defence, parental care, round goby, smallmouth bass.

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INTRODUCTION

Providing parental care is costly and, therefore, invokes trade-offs among components of fitness (Lack, 1947; Williams, 1966; Trivers, 1972). Trade-offs in parental care for birds have been considered to be a balance between offspring number and offspring survival, resulting in an optimal clutch size (Lack, 1947). Lack's (1947) ideas, however, dealt with trade-offs only within a breeding season. Williams (1966) elaborated on Lack's idea, but proposed that the more important trade-off is between current and future fitness. That is, organisms must balance the value of their current brood against the fitness gained from their future reproductive efforts to maximize their lifetime reproductive fitness. Thus, an individual investing too heavily in its current brood may sacrifice future reproductive gains (Williams, 1966; Trivers, 1972; Gustafsson and Sutherland, 1988).

The risks and costs of parental care affect the balance between current and future fitness and vary depending on reproductive behaviour and environment. When faced with a high risk of nest detection and death by visiting or guarding their brood, parents in high predation-risk environments provide less care than parents in low predation-risk environments, especially in populations where adult survival is already low (Ghalambor and Martin, 2000, 2002; Mallory *et al.*, 1998). In species in which extra-pair fertilizations occur, low or uncertain relatedness also may cause parents to provide less care than when relatedness and thus fitness are high (Mauck *et al.*, 1999; Östlund-Nilsson, 2002; Neff, 2003). Energetic expenditures on parental care can reduce adult survival, growth, and future fitness (Townshend and Wootton, 1985; Ridgway, 1986; Sabat, 1994; Balshine-Earn, 1995). Consequently, when the energetic cost of parental care increases or food availability decreases, parents are more likely to abandon their current reproductive effort (Townshend and Wootton, 1985). However, when parents are caring for a brood that is either large or near independence, they are more likely to accept the cost of providing care, and even provide more intense care, than when their brood is small or young (Coleman *et al.*, 1985; Ridgway, 1988, 1989; Coleman and Fischer, 1991; Skolbekken and Utne-Palm, 2001).

We chose to explore reproductive decisions using smallmouth bass, *Micropterus dolomieu*. Male smallmouth bass provide parental care for their offspring by fanning the nest to provide oxygen and defending the nest from potential predators. Providing care is energetically costly for smallmouth bass due to direct energetic expenditures on nest defence (Gillooly and Baylis, 1999; Mackereth *et al.*, 1999; Steinhart *et al.*, 2005b) and, indirectly, because providing care may limit foraging opportunities (Hinch and Collins, 1991). Although prematurely abandoning a nest will result in total brood failure, it does allow smallmouth bass to spend more time feeding during spring and summer. Indeed, spawning smallmouth bass experience lower annual survival than non-spawning individuals (Ridgway, 1986; Dunlop *et al.*, 2005a). In addition, foregoing reproduction for increased growth could result in larger size at next reproduction, which is important because smallmouth bass are size assortative spawners and large males receive more eggs than small males (Wiegmann *et al.*, 1992; Mackereth *et al.*, 1999). Males may abandon a brood and attempt to spawn again within a year, but repeat spawning is costly (Székely and Cuthill, 2000) and not common in smallmouth bass. Other factors that might influence smallmouth bass nest abandonment decisions include reproductive lifespan, probability that a nest will be destroyed by stochastic events, and offspring daily survival.

To understand how this complex suite of interactions affects reproductive decisions, we used dynamic programming to simulate when brood abandonment is the optimal choice for individual smallmouth bass in two lakes that differed in smallmouth bass growth, survival, cost of care, and probability of nest success. We explored how brood abandonment varies

with parental state and under different environmental conditions found in two lakes. In one of these lakes, the round goby (*Neogobius melanostomus*), a recently arrived non-indigenous nest-predator (Charlebois *et al.*, 1997), poses a new pressure on smallmouth bass reproduction; hence, we examined how this novel nest predator might change smallmouth bass brood abandonment. Dynamic programming is ideally suited for addressing these types of questions because it identifies the behaviours, based on an individual's current state, that optimize lifetime reproductive fitness (Mangel and Clark, 1988). We hypothesized that: (1) when factors that increase the probability of future reproductive success (i.e. adult survival rate, probability of nest success, and offspring survival) are high, parents will be more likely to abandon their current brood than when those factors are low; (2) when the costs or risks of providing care decrease future reproductive success (i.e. high energetic costs or probability of death while providing care), parents will abandon large broods they would normally guard if the cost of care is low; and (3) lake-specific environmental conditions should result in different optimums of parental behaviour.

METHODS

Smallmouth bass reproductive ecology

Male smallmouth bass are iteroparous and are the sole providers of parental care for their developing offspring. In spring, as water temperatures approach 15°C, male smallmouth bass clear an area for a nest, usually over cobble. After the female deposits her eggs, the male remains to guard developing offspring as the young pass through several developmental stages. As embryos, smallmouth bass are non-mobile and, therefore, extremely vulnerable to nest predators. During this stage, the male chases potential predators and fans the nest to provide oxygen and clear the nest of debris (Ridgway, 1988; Hinch and Collins, 1991). Even after the offspring develop into free-swimming larvae, males provide constant care until larvae metamorphose into juveniles. The total duration of care ranges from 17 to 43 days (Ridgway and Friesen, 1992; Knotek and Orth, 1998). Providing care causes nesting males to lose energy and weight (Gillooly and Baylis, 1999; Mackereth *et al.*, 1999; Steinhart *et al.*, 2005b). As with many fishes, providing care can reduce future fecundity and decrease parental survival, but is required or the offspring will perish (Ridgway, 1986).

Study sites

We studied nesting smallmouth bass in Lake Erie, Ohio, USA, and in Lake Opeongo, Ontario, Canada, to estimate parameters necessary for our model. In mesotrophic Lake Erie, we surveyed nesting smallmouth bass in the Bass Islands, located in the western basin of the lake (41°40'N, 82°50'W), during May and June 1999–2001. In oligotrophic Lake Opeongo (45°42'N, 78°22'W, Algonquin Park, Ontario), we observed nesting smallmouth bass during June 2001 and used published data to obtain appropriate parameter values.

Lake Erie and Lake Opeongo were chosen as contrasting systems because they differ in factors that may affect smallmouth bass life history and reproductive behaviour. Smallmouth bass are native to Lake Erie, but were introduced into Lake Opeongo in the early 1920s, rapidly establishing a self-sustaining population (Ridgway, 1986; Shuter *et al.*, 1987). Both angling and harvest of spawning smallmouth bass were allowed in Lake Erie prior to 2004, although harvest has been prohibited since 2004. Fishing during spawning is prohibited in

Lake Opeongo. Lake Erie has a more productive and longer growing season than Lake Opeongo and smallmouth bass grow faster in Lake Erie than in many other lakes (Doan, 1940). As a result of differences in fishing pressure, and possibly growth rate, adult survival is generally lower in Lake Erie than in Lake Opeongo (R. Knight, personal communication, 2004; Dunlop *et al.*, 2005a, 2005b; Ridgway, 1986). Lakes Erie and Opeongo also differ in nest-predator densities, with smallmouth bass progeny experiencing a higher risk of nest predation in Lake Erie than in Lake Opeongo (Steinhart *et al.*, 2004). Storms, by creating waves, depositing sediment, and causing temperature fluctuations, are significant sources of nest failures in both lakes (Goff, 1986; Friesen, 1998; Steinhart *et al.*, 2005a). Lake Erie, owing to its large fetch, is exposed to more violent storms than Lake Opeongo, and thus has lower nest success (Steinhart *et al.*, 2005a). Given that smallmouth bass in Lake Erie, with respect to Lake Opeongo, experience a lower survival rate (i.e. less likely to reproduce again), a lower probability of nest success (i.e. nest predators reduce offspring survival and storms destroy nests), and can recover the cost of parental care more easily because of high growth, we expected that males would be willing to guard smaller broods in Lake Erie than in Lake Opeongo.

Model summary

We built a dynamic programming model that predicted optimal behaviour of nest-guarding smallmouth bass. The model is based on the assumption that guarding males will behave such that they maximize their lifetime fitness, herein defined as the number of offspring surviving until metamorphosis. Using backward iteration (Mangel and Clark, 1988), the dynamic programming model predicted whether males should abandon or guard broods based on a male's state: his age, brood age, and brood size. In daily time steps, the model calculated expected offspring production for the remainder of a male's lifetime (i.e. expected future fitness) if he guarded or abandoned his current brood and, then, males selected the behaviour that maximized their lifetime fitness. Abandonment caused males to gain no fitness for that year. Thus, for abandonment to be an advantageous behaviour, there must be some cost to providing care. In our model, the direct costs of care for guarding males were reductions in survival and growth, the latter resulting in lower future fecundity. An indirect cost of care was the increased probability of being captured and killed by an angler, as we assumed non-nesting males were not vulnerable to angling. This assumption is based on the observation that bass anglers are known to target spawning areas in Lake Erie while the males are providing care. Therefore, males away from the spawning area are less likely to be captured. During each day, nest-guarding males lost a fixed proportion of offspring to natural mortality, had some probability of being caught and, if caught, kept (resulting in death of the brood and the male) or released (resulting in brood reduction by nest predators). On each day, nests had a probability of being destroyed by a storm. If parental care was successfully completed, males added their current brood to their lifetime fitness and then had to survive until the next year before spawning again.

Our base models simulated behaviour of male smallmouth bass from Lake Erie, before the invasion of round gobies, and Lake Opeongo. We used these models to explore how male state affects optimal decisions and expected lifetime fitness. Next, we tested model sensitivity to several different parameters to determine which factors had the most influence on optimal behaviour and to understand how differences in the suite of conditions that characterize Lakes Erie and Opeongo (angling, growth rates, probability of nest success,

etc.) interact to affect brood abandonment thresholds. Because we suspected that the most influential difference between the lakes was the presence of round gobies and their interactions with angling effects, we compared optimal decisions in both lakes in simulations with and without round gobies. Finally, we investigated which parameters were most important in determining brood abandonment by changing parameters in Lake Erie simulations in a step-wise fashion in an attempt to make Lake Erie smallmouth bass behave similarly to those in the Lake Opeongo simulation.

Model derivation

On each simulation day d ($d = 1, 2, \dots, D - 1$) of every spawning season y ($y = 1, 2, \dots, Y$), a male smallmouth bass first made the decision to guard or abandon his brood, based on expected probabilities of future events influencing current and future fitness. Next, males lost offspring to natural mortality, then had some probability of being caught by an angler and, finally, had some probability of losing their entire brood to a storm. At the start of the last day D of any season, offspring left the nest and males received fitness equal to their current brood size (B) on that day; males did not make a decision or experience reductions in offspring on day D . A male's behavioural decision was made based on his state: his current brood size (B), brood age (d), and his age (y). We used male age (in years) as a state variable because age affects the probability of surviving to reproduce another year. Age also was a surrogate for male size (total length, TL , in millimetres). Male total length was estimated from length-at-age relationships specific to either Lake Erie or Lake Opeongo (Table 1). In turn, male size was positively related to the number of eggs he received (Wiegmann *et al.*, 1992; Mackereth *et al.*, 1999). We calculated starting brood size on day $d = 1$ (B_0) for males of different ages from a total length–brood size relationship:

$$B_0 = a \cdot TL + b, \quad (1)$$

where the coefficients a and b varied by lake [Table 2; male size–brood number relationship from G.B. Steinhart and M.S. Ridgway (unpublished data)]. We considered brood size in 100 offspring increments when calculating brood size at the start of the day (i.e. brood size rounded to nearest 100), and used linear interpolation for values between these increments when calculating expected future fitness.

Males began day d with brood size B , and made the decision to guard or abandon based on expected future fitness, which was a combination of several probabilistic events. Many smallmouth bass offspring die from disease, predation, and anoxia (Friesen, 1998; Knotek and Orth, 1998), but daily survival varies with offspring age, so we included separate embryonic ($d = 1$ –13) and larval ($d = 14$ –20) daily survival rates (DSR ; Table 2). Next, guarding males had a fixed, daily probability of capture by an angler (p_A ; Table 2). In simulations in which smallmouth bass harvest was allowed, males were released with a size-dependent probability (p_R), because anglers often are more likely to release small fish than large fish:

$$p_R = 1 - i \cdot e^{j \cdot TL}, \quad (2)$$

where coefficients i and j varied by lake (Table 2). Where harvest was prohibited (i.e. the base simulation in Lake Opeongo), $p_R = 0.99$. When a male was caught and kept, the entire brood failed. If caught and released when round gobies were present, males lost 800

Table 1. Age-dependent parameter values for male smallmouth bass included in the stochastic dynamic programming model

Lake Erie					Lake Opeongo				
Age	<i>TL</i>	<i>B</i>	<i>ASR</i>	ΔASR	Age	<i>TL</i>	<i>B</i>	<i>ASR</i>	ΔASR
3	303	2999	0.59	0.004	3	N.A.	N.A.	N.A.	N.A.
4	342	3539	0.55	0.0008	4	259	871	0.7	0.025
5	372	3957	0.47	0.0005	5	280	1145	0.6	0.015
6	396	4299	0.39	0.0005	6	300	1403	0.5	0.008
7	417	4589	0.31	0.0005	7	322	1691	0.45	0.0015
8	435	4839	0.21	0.0005	8	350	2051	0.4	0.001
9	450	5060	0.11	0.0005	9	372	2342	0.4	0.001
10	465	5258	0.07	0.0005	10	395	2640	0.4	0.001
11	473	5380	0.04	0.0005	11	411	2839	0.3	0.001
12	485	5544	0.02	0.0005	12	430	3095	0.2	0.001
13	496	5694	0.01	0.0005	13	445	3286	0.1	0.001
14	504	5810	0.01	0.0005	14	458	3457	0.05	0.001
15+	510	5894	0.01	0.0005	15+	465	3545	0.01	0.001

Note: Smallmouth bass in Lakes Erie and Opeongo had a different age range (i.e. no age-3 spawning males in Lake Opeongo), total length at age (*TL*, in mm), initial brood size (*B*), adult annual survival rate (*ASR*), and cost of parental care (ΔASR ; daily reduction in *ASR* when guarding).

Table 2. Lake-specific parameters for a stochastic dynamic programming model of nest-guarding male behaviour in Lakes Erie and Opeongo

Parameter	Lake Erie	Lake Opeongo
$B_0 = a \cdot TL + b$	$a = 14, b = -1246$	$a = 13, b = -2500$
<i>DSR</i> (embryos, larvae)	0.90, 0.92	0.90, 0.92
p_s	0.065	0.015
p_A	0.05	0.01
$p_R = 1 - i \cdot e^{j \cdot TL}$	$i = 0.01, j = 0.007$	0.99
Offspring consumed during angling	0	0
ΔTL	0.8	0.5

Note: Values shown are for base simulations in each lake: age-specific brood size (B_0), daily survival rate (*DSR*), probability a nest was destroyed by a storm (p_s), probability an angler captures a male (p_A), probability a male is released if caught (p_R), offspring consumed during angling, and daily cost of care in male total length (ΔTL).

offspring to nest predators (Steinhart *et al.*, 2004). Thus, a male that guarded his brood and was not caught on day *d* began with brood size B' on day *d* + 1:

$$B' = B \cdot DSR. \quad (3)$$

But a male that guarded his brood and was caught and released on day *d* began with brood size B'' on day *d* + 1

$$B'' = \begin{cases} B' - 800, & \text{with round gobies} \\ B', & \text{without round gobies} \end{cases}. \quad (4)$$

In addition, because storms can destroy many smallmouth bass nests (Goff, 1986; Friesen, 1998; Steinhart *et al.*, 2005a), we included the daily probability a nest was destroyed by a storm (p_S ; Table 2). Destruction of a nest did not affect the male, but did result in total brood failure (B' and $B'' = 0$).

Our model incorporated parental care costs because providing care causes male smallmouth bass to lose weight and energy (Mackereth *et al.*, 1999; Steinhart *et al.*, 2005b). Our model used male length instead of weight or energetic content, so we modelled care costs as a decline in total length (ΔTL ; Table 2) for each day of care. Although field data do not show a decline in length during the spawning season, males did lose energy content (Steinhart *et al.*, 2005b), which we modelled by assuming a reduction in male size at the beginning of the next spawning season (from the expected lengths in Table 1). Because starting brood size B_0 was a function of total length (equation 2), a new starting brood size B'_0 for year $y + 1$ was calculated based on whether a male guarded or abandoned on day d in year y :

$$B'_0 = \begin{cases} a \cdot TL - \Delta TL \cdot d + b, & \text{if male guards} \\ a \cdot TL - \Delta TL \cdot (d - 1) + b, & \text{if male abandons} \end{cases} \quad (5)$$

with a and b defined as for equation (1). In addition, providing care reduces annual survival rate; nesting males experience lower annual survival (ASR) than non-nesting males (Ridgway 1986; and from spawning surveys described in Dunlop *et al.* 2005a, 2005b). In our model, adult ASR was age-dependent, decreasing with male age, and we included a daily reduction of annual survival rate (ΔASR ; Table 1) for males providing care.

Expected future fitness for a male of age y with brood of size B on day d , $F(B, d, y)$, is made up of the probabilities of different events multiplied by the expected fitness value if each of those events occurred. The expected fitness value (V) varied based on male decisions and probabilistic events. For a male making the decision to guard on day d and then not encountering a storm or an angler that day, the expected fitness value is:

$$V_0 = F(B', d + 1, y). \quad (6)$$

The expected fitness of deciding to guard on day d and then encountering a storm, if a male is not caught and kept by an angler, is his probability of surviving to the next nesting season and his expected fitness from that point on:

$$V_S = (ASR - \Delta ASR \cdot d)F(B'_0, 1, y + 1). \quad (7)$$

The expected fitness of deciding to guard the nest when a male is caught and released by an angler, given that the brood is not destroyed by a storm, is:

$$V_{A,R} = F(B'', d + 1, y). \quad (8)$$

If a male is caught and kept by an angler, regardless of whether his brood is destroyed by a storm, his expected fitness is 0.

If a male abandons his brood, the expected fitness is determined by his probability of surviving to the next nesting season and his expected fitness from that point on is:

$$V_{ab} = (ASR - \Delta ASR(d - 1))F(B'_0, 1, y + 1). \quad (9)$$

These expected fitness values (equations 6–9) result in the following expected future fitness on day d :

$$F(B, d, y) = \begin{cases} \text{Guard: } (1 - p_s)[(1 - p_A)V_0 + p_A p_R V_{A,R}] + p_s V_s \\ \text{Abandon: } V_{ab} \end{cases} \quad (10)$$

On the last day D of each nesting season $y < Y$, offspring left the nest, males received fitness equal to their brood size, and expected future fitness is:

$$F(B, D, y) = B + (ASR - \Delta ASR \cdot D)F(B'_0, 1, y + 1). \quad (11)$$

On the last day D of the last spawning season Y , expected future fitness is:

$$F(B, D, y) = B. \quad (12)$$

Parameterization of simulations

Our simulation assumed 20 days of care were required to raise offspring to independence and that males could spawn once each year. Duration of parental care within a season is variable and temperature dependent (Friesen, 1998). It is generally assumed that parental care may end, and the offspring survive, once offspring metamorphose into juveniles (Ridgway, 1986), requiring anywhere from 14 to 43 days (Friesen, 1998; Knotek and Orth, 1998). Our simulations assumed that developing offspring would metamorphose at the start of day 21. Male smallmouth bass begin spawning at age 3 in Lake Erie and age 4 in Lake Opeongo (G.B. Steinhart, unpublished data; Ridgway 1986; Dunlop *et al.*, 2005a, 2005b); however, because only a few males reproduce at these ages, most comparisons were made with males spawning at age 4 (Lake Erie) and age 5 (Lake Opeongo). Males over age 13 are rarely seen in either lake, but to avoid effects of an artificially constrained lifespan, the model allowed fish to spawn for 20 years ($Y = 20$), reaching age 23 in Lake Erie and age 24 in Lake Opeongo, in the very unlikely event that they survived that long.

For males of a given age, length (TL) was estimated from catch-at-age data. Males in Lake Erie were larger at any given age than males in Lake Opeongo (Table 1). We assumed males reached their maximum TL at age 15 years in both lakes, thereafter maintaining a constant length. For the base simulations, brood size on day 1 (B_0), probability of release if caught (p_R), adult annual survival rate (ASR), and change in annual survival by providing care (ΔASR) were related to age-specific TL (Tables 1 and 2). Daily probability that an angler caught a guarding male, p_A , for base simulations was 0.05 in Lake Erie and 0.01 in Lake Opeongo. We calculated age-specific p_R (equation 2) that, when weighted by abundance of smallmouth bass of all ages in Lake Erie, yielded a mean release probability of 0.2, approximating mean release rate from Lake Erie creel surveys (R. Knight, Ohio Division of Wildlife, unpublished data). When simulating a no-fishing situation (the base condition in Lake Opeongo), p_R was 0.99. Base offspring daily survival rate (DSR) was 0.9 for embryos ($d = 1-13$) and 0.92 for larvae ($d = 14-20$), based on values from Lake Opeongo and elsewhere (Friesen, 1998; Knotek and Orth, 1998).

The daily probability that a nest was destroyed by a storm, p_s , was estimated from smallmouth bass nests monitored *in situ* in both lakes (Steinhart *et al.*, 2005a). Base p_s values were 0.065 in Lake Erie and 0.015 in Lake Opeongo (Table 2).

We estimated parental care costs (ΔTL and ΔASR) from empirically measured changes in wet weight (converted to change in TL) in Lake Erie, with round gobies present, and from

changes in wet weight and annual survival in Lake Opeongo (Ridgway, 1986; Dunlop *et al.*, 2005a; Steinhart *et al.*, 2005b). Activity level of nest-guarding males in Lake Erie, with round gobies present, was about 2.5 times higher than that in Lake Opeongo where round gobies were not present (Steinhart *et al.*, 2005b). Therefore, we assumed that when round gobies were absent, the cost of care would be only 40% (i.e. $1/2.5$) the cost when round gobies were present. In Lake Erie, we measured ΔTL as 2 mm per day of care when round gobies were present and adjusted ΔTL to 0.8 mm per day of care without round gobies. In Lake Opeongo, we measured ΔTL as 0.5 mm per day of care. Change in annual survival, ΔASR , varied by male age and was based on annual survival differences between nesting and non-nesting males in Lake Opeongo (Table 1) (Ridgway 1986; Dunlop *et al.*, 2005a, 2005b). We arrived at Lake Erie ΔASR by first using the ΔASR from a similar length smallmouth bass in Lake Opeongo; then, because high growth rates in Lake Erie likely reduce the cost of care on annual survival compared with Lake Opeongo, we reduced ΔASR values by half. For all simulations, ASR could not drop below 0.01 after adjustments for parental care.

Model simulations

After running base simulations for Lakes Erie and Opeongo with parameters as defined above, we ran a series of simulations to understand how model parameters affected smallmouth bass brood abandonment. For these simulations, we changed only one parameter at a time, keeping other conditions as described for the base simulations. First, we looked at parameters that affected the fitness value of broods within a spawning season. In each lake, we varied: (1) daily probability that a nest was destroyed by a storm (p_s) by halving and doubling the base values; (2) offspring daily survival rate (DSR) by ± 0.05 ; and (3) adult survival within the spawning season by varying the probability that a male was caught from its nest while guarding ($p_A = 0.01, 0.05, 0.1$). Because the base model in Lake Opeongo assumed that 99% of males caught by anglers were released, when we tested the effect of angling during the spawning season in Lake Opeongo, we allowed harvest by assuming that anglers in Lake Opeongo kept smallmouth bass with p_R calculated from equation (2), with parameters $i = 0.01$ and $j = 0.009$. These parameter values resulted in a mean p_R similar to Lake Erie. Next, we looked at parameters that affected fitness across spawning seasons by: (1) changing adult annual survival by varying ASR by ± 0.1 , and (2) altering the cost of parental care, which affected both ΔTL and ΔASR , by running simulations with no care costs and double the care costs in each lake.

To examine how nest predation might affect smallmouth bass brood abandonment in both lakes, we ran simulations with round gobies in each lake. Although round gobies are not present in Lake Opeongo, they have invaded inland lakes in Ontario. When including round gobies in our simulations, we assumed round gobies consumed 800 offspring every time a male was caught and released by an angler (Steinhart *et al.*, 2004). In addition, we modified the cost of parental care when round gobies were present, because round gobies increased energetic losses for nest guarding males in Lake Erie (Steinhart *et al.*, 2005b). For Lake Erie, we used the daily change in male wet weight while guarding when round gobies were present and converted it to ΔTL (2 mm per day of care). Again, because activity level of nest guarding males in Lake Erie was higher than standard metabolism when round gobies were present (Steinhart *et al.*, 2005b), we assumed ΔASR would be 2.5 times higher in both lakes than in base simulations (Table 1).

Finally, once we observed the base results from each lake, we changed parameters to force male smallmouth bass in Lake Erie to behave similarly to male smallmouth bass in Lake Opeongo. Our objective was to determine which parameters were most important in defining underlying differences in brood abandonment in the two lakes. We began with the base simulation in Lake Erie and then changed model parameters and examined their effects on brood abandonment. To the base Lake Erie simulation, we individually added Lake Opeongo values for (1) angling (both p_A and p_R), (2) ASR , (3) p_S , (4) ΔTL , and (5) ΔASR . We ran simulations in Lake Erie in a step-wise fashion with different combinations of these parameter values from Lake Opeongo until we determined the minimum set of parameters that produced optimal behaviours in Lake Erie that were most similar to optimal behaviours in Lake Opeongo.

RESULTS

Male age and brood age

Optimal older males were predicted to guard smaller broods than would young males, but the difference in age-specific abandonment thresholds varied by lake (Fig. 1). In Lake Erie simulations, males aged 3–5 abandoned their nests only when their broods became extremely small, but in Lake Opeongo, males abandoned their broods after only slight reductions in brood size. In fact, our model predicted that if an average age 4 male

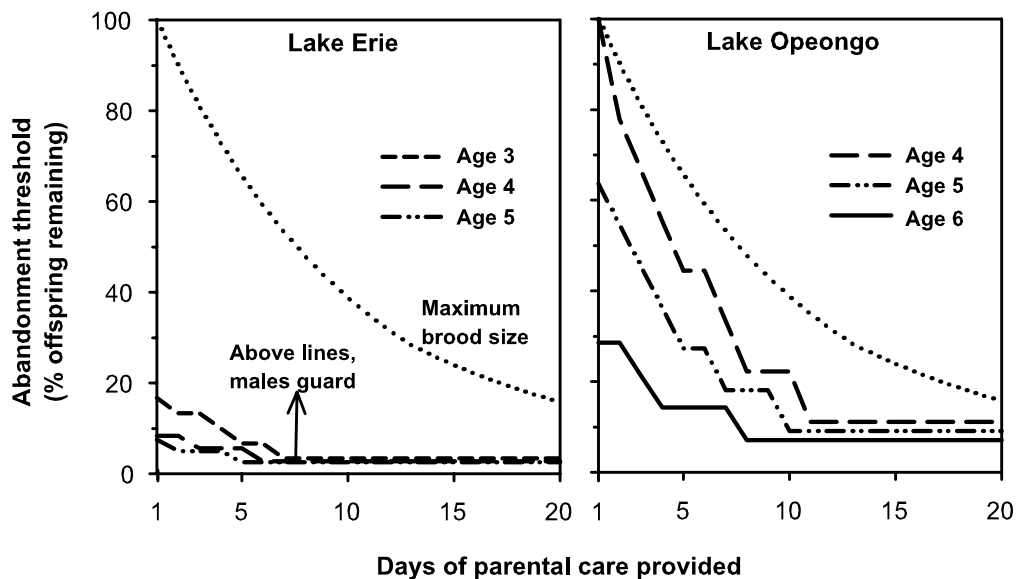


Fig. 1. Optimal male smallmouth bass reproductive behaviour (guard or abandon current brood) as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) in Lake Erie and Lake Opeongo. Solid and dashed lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Dotted lines show the maximum percentage of the starting brood size remaining, given normal daily egg and larval mortality in the nest. Results are displayed for the first 3 years in which at least some males are reproductively mature in each lake.

in Lake Opeongo were to spawn (they often do not), he would always choose abandonment on day 1. Males aged 5 and 6 would abandon in Lake Opeongo only if their broods reached 65% and 30% of initial brood size respectively. In addition, as days of care provided increased, optimal male smallmouth bass were predicted to guard even very small broods (Fig. 1).

In-season storms and offspring daily survival rate

Reduction in daily probability p_S of nest destruction by storms caused little difference in brood abandonment (Fig. 2). Note that it is important to remember that our brood size increment was 100 offspring; thus, the smallest percentage of offspring remaining in our models was 3% for an age 4 male in Lake Erie and 9% for an age 5 male in Lake Opeongo. Therefore, abandonment might occur anywhere from one offspring to 3% (Lake Erie) or 9% (Lake Opeongo) of offspring remaining. Although abandonment thresholds were not sensitive to probability of storms, daily probability of nest destruction by storms did have a large effect on expected lifetime fitness of male smallmouth bass in Lake Erie. Under base storm probability, optimally behaving males had an expected lifetime offspring production of 205 in Lake Erie and 148 in Lake Opeongo, but when p_S was halved, expected offspring production dropped to 51 in Lake Erie and 120 in Lake Opeongo.

Changing offspring daily survival rate DSR altered brood abandonment thresholds in Lake Opeongo, but not in Lake Erie (Fig. 2). With increased offspring daily survival, males in Lake Opeongo abandoned broods that were normally guarded. Elevated offspring daily survival increased expected lifetime fitness in both Lake Erie (from 205 to 600 offspring) and Lake Opeongo (from 148 to 426 offspring).

Adult survival

In both Lakes Erie and Opeongo, decreasing the probability p_A that a male was angled from its nest caused little change in optimal abandonment behaviour (Fig. 3). Although the difference was small, the predicted change was in the opposite direction in each lake. In Lake Erie, decreasing p_A reduced the abandonment threshold to the point that optimal males should always guard their brood. In Lake Opeongo, however, slightly larger broods might be abandoned when the probability of being caught by an angler is low (Fig. 3). In both lakes, there was relatively little change in expected future lifetime fitness when p_A was increased: 167, 205, and 245 offspring in Lake Erie and 115, 130, and 145 offspring in Lake Opeongo for $p_A = 0.01, 0.05$, and 0.1 , respectively.

Changing adult annual survival rate ASR by ± 0.1 caused little change to brood abandonment in Lake Erie but optimal males in Lake Opeongo might abandon larger broods when adult annual survival was high (Fig. 3). Although increased adult annual survival only slightly raised the abandonment threshold in Lake Erie, increasing adult survival by reducing angling probability – and, therefore, harvest – led to the opposite effect (Fig. 3). Increasing adult annual survival by 0.1 increased expected future lifetime fitness from 205 to 245 offspring in Lake Erie and from 148 to 204 offspring in Lake Opeongo.

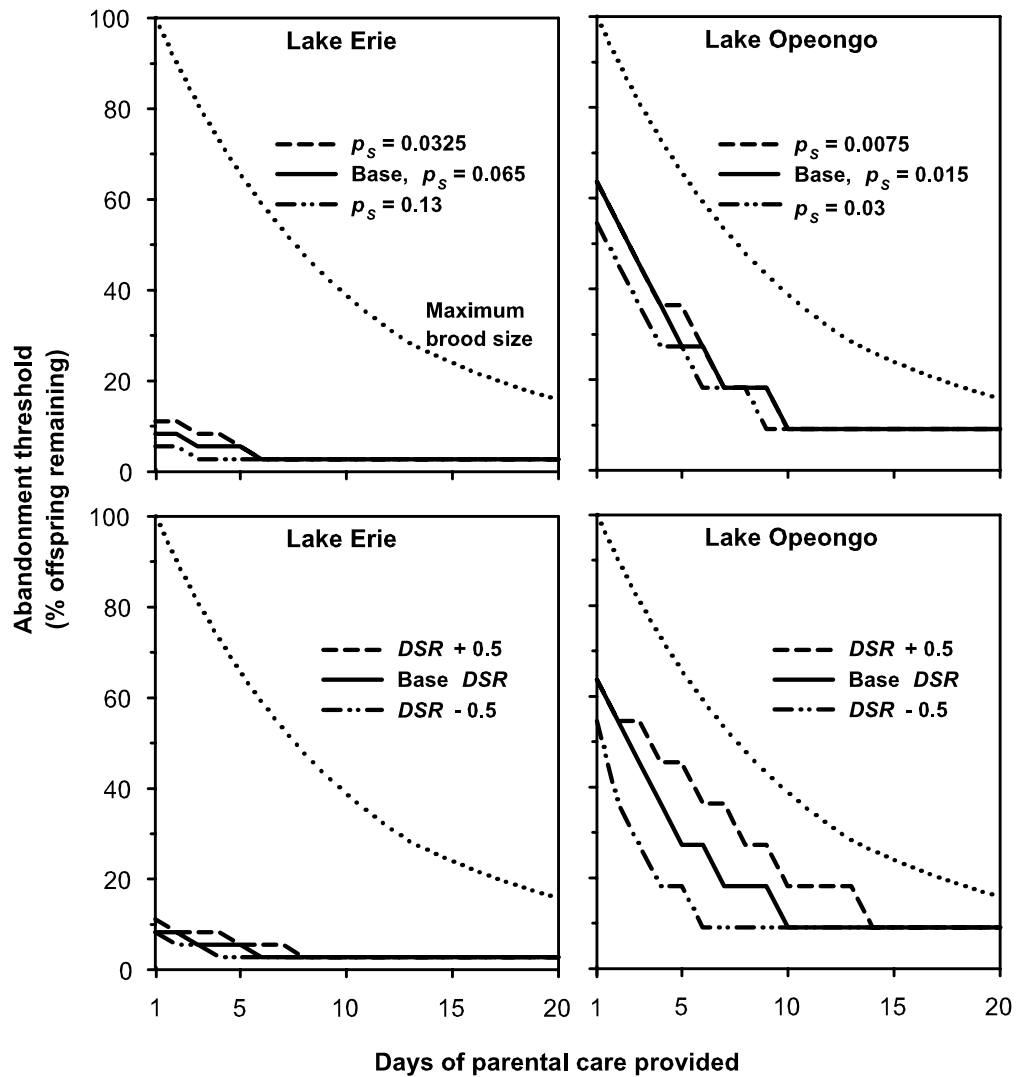


Fig. 2. Optimal smallmouth bass behaviour as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) under different daily probabilities that a nest was destroyed by a storm (p_s) and different offspring daily survival rates (DSR). Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Solid and dashed lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Dotted lines show the maximum percentage of the starting brood size remaining, given normal daily egg and larval mortality in the nest.

Cost of parental care

Removing all costs of parental care suggested that optimal male smallmouth bass should always guard their broods in Lake Opeongo (Fig. 4). In Lake Erie, where base parental care costs were lower than in Lake Opeongo, removing the energetic costs of parental care (ΔTL

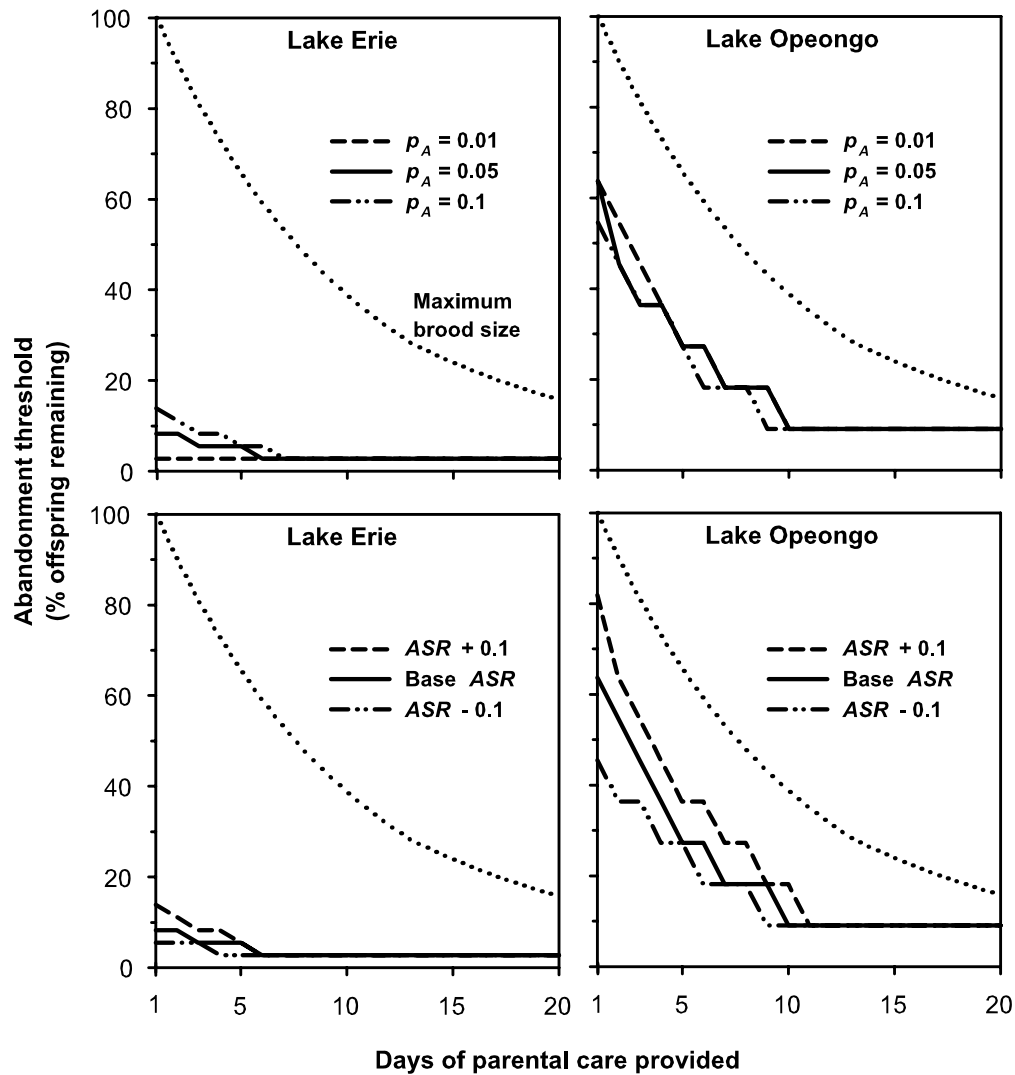


Fig. 3. Optimal smallmouth bass behaviour as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) under different daily probabilities that a male was caught by an angler (p_A) and different adult annual survival rates (ASR). Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Solid and dashed lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Dotted lines show the maximum percentage of the starting brood size remaining, given normal daily egg and larval mortality in the nest.

and ΔASR) made only a small difference in the abandonment threshold. Because we simulated different base care costs (i.e. higher in Lake Opeongo) and, possibly, differential risk of being caught by an angler while guarding (i.e. lower in Lake Opeongo), decreasing the cost of care had a greater effect on expected lifetime fitness of optimal males in Lake Opeongo (104, 148, and 309 expected future offspring with double cost, base cost, and no cost respectively) than in Lake Erie (192, 205, and 219 expected future offspring).

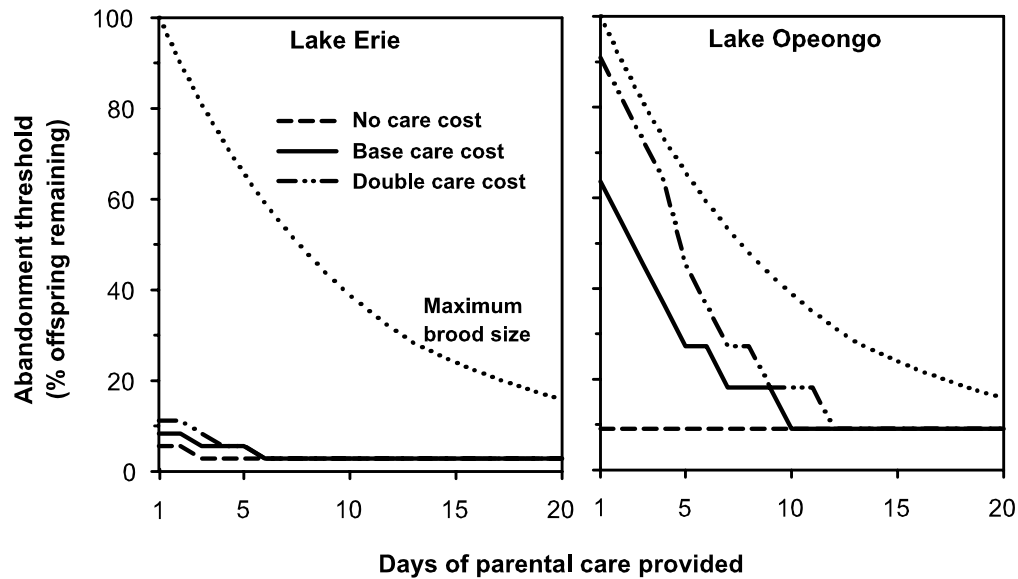


Fig. 4. Optimal smallmouth bass behaviour as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) under different parental care costs. Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Solid and dashed lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Dotted lines show the maximum percentage of the starting brood size remaining, given normal daily egg and larval mortality in the nest.

Nest predators

Adding nest-depredating round gobies to our simulations led optimal males to abandon their nests with slightly more offspring remaining than if round gobies were absent (Fig. 5). Changes in brood abandonment thresholds were greatest in Lake Opeongo, most likely because the round goby-adjusted cost of parental care was much higher in Lake Opeongo than Lake Erie. Round gobies decreased offspring survival by consuming offspring only when males were angled from their nests; however, the resulting change in behaviour was opposite to the effect of decreasing offspring survival DSR directly. Adding round gobies reduced expected future lifetime fitness for optimal males by 69 offspring in Lake Erie and 54 offspring in Lake Opeongo.

Forcing Lake Erie males to behave similarly to Lake Opeongo males

When we examined how changing model parameter values affected brood abandonment for Lake Erie simulations, we found that including Lake Opeongo angling probability and release probability caused optimal males in Lake Erie always to guard their broods. In fact, by reducing the risk of being caught and kept in Lake Erie, optimal males always guarded their offspring, regardless of brood size. Individually adding Lake Opeongo adult survival, daily probability of a storm destroying a nest, or cost to adult survival of providing care increased the abandonment threshold (i.e. optimal males abandoned broods they normally should have guarded). The cost to adult survival for providing care had the largest single

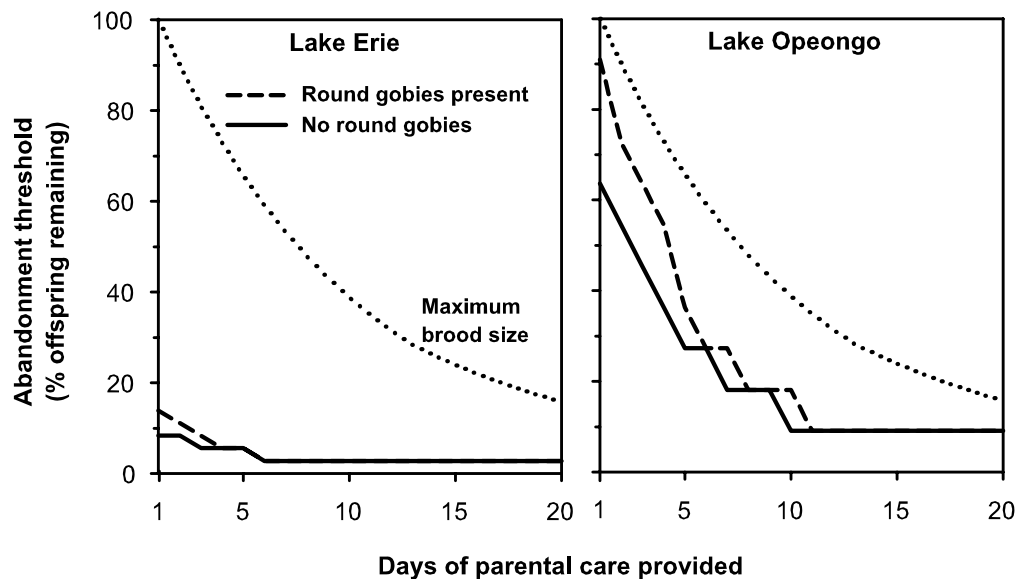


Fig. 5. Optimal smallmouth bass behaviour as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) when a nest predator, round goby, was present or absent. Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Solid and dashed lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Dotted lines show the maximum percentage of the starting brood size remaining, given normal daily egg and larval mortality in the nest.

effect, followed by daily probability a storm destroyed a nest, then adult annual survival rate. Thus, we determined that these three parameters were the important factors that led to differences in brood abandonment between the two lakes. When we changed these three parameters in the Lake Erie simulation to Lake Opeongo values in a step-wise fashion, the cost of care to adult survival (ΔASR) from Lake Opeongo raised the abandonment threshold in Lake Erie (Fig. 6). Adding Lake Opeongo probability that a storm destroyed a nest (p_S) to the Lake Erie simulation made little difference to the abandonment threshold, but adding Lake Opeongo adult annual survival rate (ASR) to both of these resulted in similar abandonment thresholds in both systems (Fig. 6). Without changing length-at-age or total length–brood size relationships between lakes, changing these three parameters in Lake Erie simulations resulted in the closest match in abandonment behaviour, even when we added more Lake Opeongo parameter values to the Lake Erie model.

DISCUSSION

Optimal male behaviour was predicted to differ between Lake Erie and Lake Opeongo. Our model found that optimally behaving males in Lake Erie should rarely abandon their broods, even when their broods become very small. In contrast, optimally behaving males in Lake Opeongo should be more prone to abandoning their nests. Experimental manipulations in the field support the proposition that smallmouth bass brood abandonment thresholds vary by system. Limited brood reduction experiments in Lake Erie found

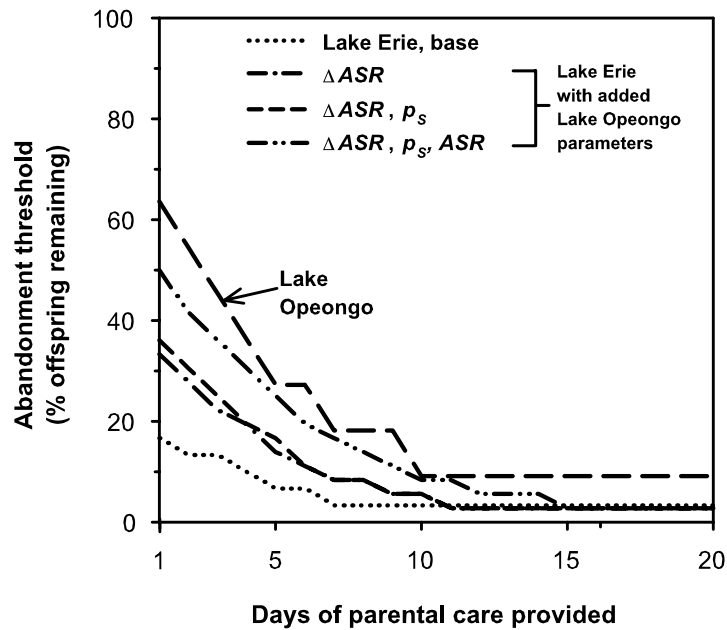


Fig. 6. Optimal smallmouth bass behaviour as a function of current brood size (B , as a percentage of starting brood size B_0) and days of care already provided (d) for an age-4 male in Lake Erie, but with the addition of model parameter values from Lake Opeongo. To the base Lake Erie simulation, we added, step-wise, Lake Opeongo values for cost to annual adult survival of providing care (ΔASR), probability that a nest was destroyed by a storm (p_S), and adult annual survival rate (ASR) to try to force an optimal age-4 male in Lake Erie to behave as an optimal age-5 male in Lake Opeongo (i.e. males in their second year of spawning in both lakes). Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.

10 of 11 males continued to guard their nests (mean of 6 days after brood reduction) until a storm occurred (G.B. Steinhart, unpublished data). Preliminary brood reduction experiments in Lake Opeongo suggested no change in nest abandonment rate by reduction amount (0, 25, 50, and 75%); however, only four reductions were done under conditions where the model predicted males should have abandoned and three of those nests were abandoned (G.B. Steinhart, unpublished data). In addition, over a 20-year period in Lake Opeongo, nest survival was higher for large males than small males (Suski and Ridgway, 2007). Finally, in Charleston Lake, Ontario, 68% of smallmouth bass nests experiencing a 50% brood reduction were abandoned, while 0% of control nests were abandoned (Suski *et al.*, 2003). Suski *et al.* (2003) found that small males were more likely to abandon than large males and that anti-predator behaviour by guarding parents decreased following brood reductions. In short, these studies show a range of responses to brood reduction: from unlikely to abandon in Lake Erie, to abandonment under specific conditions in Lake Opeongo (young males with nests early in parental care), to a relatively high abandonment rate following brood reduction in Lake Charleston.

Why do some individuals abandon their brood more readily than others? Our model suggests that differences in abandonment thresholds are likely to be a consequence of underlying differences in the characteristics of each smallmouth bass population and their

environment. For example, smallmouth bass in Lake Erie had a low annual survival due, in part, to angling and harvest. Therefore, they were less likely to reproduce in the future than were males in Lake Opeongo. As a result, males in Lake Erie placed a high value on their current broods and were less likely to abandon than were males in Lake Opeongo. This is consistent with previous life-history theory, which predicts that parental effort should increase as adult annual survival and residual reproductive value decrease (Clark *et al.*, 2002) and stresses the importance of terminal investment (Clutton-Brock, 1984; Pärt *et al.*, 1992).

Interestingly, when increasing the costs of care (i.e. by reducing annual survival), males abandoned larger broods than when care costs were normal or reduced. Why then, in the face of reduced survival due to parental care, would males abandon more readily given that low annual survival typically increases current parental investment? First, the intrinsic annual survival is not affected by duration of parental care; however, reductions in survival due to parental care can be avoided by abandoning. Second, providing care also reduced future fecundity, via decreased growth, in our model. Therefore, males that abandon early can expect to receive more eggs in the future than males who guard. Third, there is an additional risk of death during the spawning season because anglers could sometimes keep smallmouth bass during the spawning season. The combined effect of minimizing reductions to survival, increasing expected fecundity, and decreasing angler-induced mortality should cause optimal males to abandon larger broods than normal.

The risk of mortality from fishing altered parental care behaviour but the response depended on the environment. When there was an increased risk of being harvested during the spawning season, optimal males abandoned slightly larger broods in Lake Erie than when harvest was negligible. In Lake Opeongo, however, harvesting during the spawning season had much less of an effect for the relatively low angling risk we modelled. We believe the low intrinsic annual mortality and high cost of care on adult survival masked any effects of spawning season harvest in Lake Opeongo. Therefore, in some systems, increasing parental mortality during reproductive periods (via angling or hunting) may affect reproductive success in two ways: not only will some broods fail when their parents are killed, but parents also alter their level of investment when adult survival is significantly reduced by providing care (Clutton-Brock, 1984; Pärt *et al.*, 1992; Zink, 2003). Even if regulations are in place prohibiting angling during the spawning season, angling often occurs at other times of the year. Harvesting smallmouth bass outside the spawning season would decrease *ASR* in our model, which would promote increased guarding and reduced abandonment when broods are large in both lakes. The effects of fishing are worth noting because a growing body of research has shown that harvest can induce evolution of life-history traits such as maturation schedule and growth rate (Haugen and Vollestad, 2001; Conover and Munch, 2002; Reznick and Ghalambor, 2005; Dunlop *et al.*, 2007); the results of our model indicate that harvest can also promote evolution in reproductive behaviour. Although the costs associated with parental care might counteract the selective forces of angling that cause evolution in maturation age and size (Dunlop *et al.*, 2007), we show that, depending on the system, other aspects of the smallmouth bass's life-history might be prone to fishing-induced evolutionary change.

Offspring mortality affected male abandonment thresholds only in certain situations. For example, in Lake Opeongo expected future fitness was high owing to high adult survival and a low probability of nests being destroyed or depredated. Under these conditions, decreasing offspring survival caused males to abandon larger broods than when offspring survival was low. Because male size determined starting brood number, older males received larger broods than young males. The difference between maximum ending brood size for an old

male and a young male would grow larger as offspring daily survival increases. For example, if an age 4 fish receives 1000 eggs and an age 5 fish receives 1200 eggs, then the maximum remaining brood sizes after 20 days, with a daily survival of 0.9, would be 135 and 202, respectively: a difference of 67 offspring. If daily survival were increased to 0.95, the maximum remaining brood sizes would be 377 and 566: a difference of 189 offspring. As the gap in expected fitness from the current brood and expected fitness from future broods grows, males will devalue their current brood in favour of larger broods in subsequent years. However, in systems where expected future fitness is low to begin with (e.g. Lake Erie), offspring daily survival may make little difference.

Changing the probability of nest destruction by storms had little effect on optimal behaviours in either lake. This result was contrary to our prediction, because when nest success is high, we presumed that males would be more likely to abandon their broods because it should raise their expected future fitness. The lack of a behavioural response to fluctuating probabilities of nest failure may have resulted from the overriding importance of adult annual survival to the model or because probability of nest failure was not an age-dependent variable. When parents have a similar probability of succeeding in any year, regardless of age, changing the probability that they are successful would not affect the ratio of the values of their current and future broods. Indeed, other dimensionless numbers are believed to be very important for determining reproductive behaviour (Charnov, 2000; Charnov and Skúladóttir, 2000). In contrast, most other parameters tested were either directly related to parent age and size (i.e. adult annual survival, probability of being harvested, cost of parental care) or indirectly related to age (i.e. indirect effects of offspring daily survival).

Adding an abundant nest predator, the round goby, to each lake caused optimal males to abandon larger broods than without the nest predator. Round gobies are known to increase parental care costs (Steinhart *et al.*, 2005b) and consume offspring when smallmouth bass are temporarily removed from their nests (Steinhart *et al.*, 2004). In our simulations, the effect of round gobies on parental care (increased care costs led to a higher abandonment threshold) caused more of an effect than their role as nest predators (decreased offspring survival sometimes led to a lower abandonment threshold). Because round gobies are not frequently consumed by nesting smallmouth bass, their effect on cost of parental care will not be compensated for by increased consumption of nest-guarding males (Steinhart *et al.*, 2005b). Although round gobies may never arrive in Lake Opeongo, they have been found in other inland lakes in North America.

As with any model, ours included several simplifications. Two factors we did not include in the model are seasonal timing of spawning and multiple broods. Large male smallmouth bass tend to spawn earlier than small males (Ridgway *et al.*, 1991; Wiegmann *et al.*, 1997), and differences in temperatures during offspring development can influence development rates and the duration of parental care (Friesen, 1998). Considering the timing of spawning has an interesting suite of implications for optimal parental behaviour and poses an appealing question about the optimal time to spawn. For organisms that can spawn multiple times within a year, there can be a trade-off between intra-seasonal broods and parental care (Székely and Cuthill, 2000). In Lakes Erie and Opeongo, however, few males (approximately 5%) were observed attempting a second brood (G.B. Steinhart, unpublished data). We feel that timing of spawning and multiple breeding attempts within a year are interesting issues to address in future research, but they should not influence our general conclusions about the factors that affect the threshold of brood abandonment.

CONCLUDING REMARKS

Parental care theory predicts that individuals with a high expected future fitness should be more likely to abandon their offspring than individuals with a low expected future fitness, but our model suggests this was true only for some variables affecting fitness. Optimal parental behaviour was influenced most by parameters affecting adult annual survival rate. We also found that age-dependent variables, such as fecundity, were important for optimal decisions and affected the importance of other variables, such as offspring survival, when considering the ratio of current and future expected fitness. In part, the importance of these variables was because a parent's decision to guard or abandon affected the magnitude of decrease in future survival and fecundity. On the other hand, parameters that were not age-dependent and were not influenced by the decision to abandon (i.e. storm probabilities, daily offspring mortality, nest predation) had little effect on optimal behaviour. Our results also demonstrate that abandonment thresholds should vary by environment, which has important implications for how we might manage species that provide care. In systems where parents are prone to abandonment, minimizing the factors that increase abandonment (e.g. angling, introduced predators) may have a more marked effect than in systems where parents are more likely to guard reduced broods.

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