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Potential consequences of angling on nest-site fidelity in largemouth bass

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Abstract Breeding site fidelity has evolved in many vertebrate taxa, suggesting both that site selection has an important influence on fitness potential and that the decision to reuse a nesting site is related to the individual's prior nesting success at that location. For a species that provides parental care, such as the Largemouth Bass *Micropterus salmoides*, catch-and-release angling impacts individual nesting success and fitness through physiological disturbance and by removing the nest-guarding male from its brood, thereby allowing temporary access to eggs and hatchlings by brood predators. To assess the impact of catch-and-release angling on nest site fidelity, we compared the consequences of angling on individually marked (i.e., with passive integrated transponders) nest-guarding male Largemouth Bass in Ontario. An extremely high degree of nest site fidelity in year two was observed for males that were angled only once during year one (87% within 10 m of the previous year's nest), 96.7% of which remained on the nest and completed parental care activities. There was significantly lower fidelity in year two, however, for males that were angled multiple times during year one (27% within 10m of the previous year's nest), only 5.6% of which remained on the nest and completed parental care activities. This observed difference suggests that angling nesting bass may cause them to avoid previously used nest sites and instead search for alternative sites during future reproductive seasons. This human-induced impact on nest site choice may impact the future reproductive success of those Largemouth Bass.

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Introduction

The location of a male's breeding site can be an important factor in determining its reproductive output for a given season, and if a male is successful at a particular site, it stands to reason that the male would return during successive breeding seasons (Warner 1988). Breeding site fidelity is commonplace among vertebrates and has been studied extensively in birds, which often migrate long distances to return to breeding sites (e.g., Haas 1998; Powell and Frasch 2000; Schlossberg 2009). Of late, however, there has been increased interest in fish breeding site fidelity in both marine (Feldheim et al. 2014) and freshwater (Bartlett et al. 2010) systems. From an evolutionary standpoint, for a fish to return to a previous nest site, as compared to random sites within a lake, stream, or ocean, there should be an associated fitness advantage via enhanced reproductive success. It has been suggested that nest site fidelity may offer this advantage in the form of more efficient movement, reduced neighbor conflicts, and better dominance interactions (reviewed in Piper 2011). In addition, previous nesting success at a particular site and a 'win-stay/lose-move' decision rule may determine whether or not a fish returns to its previous nest site (Switzer 1993). It follows then, that anything that might cause a male to abandon his brood prematurely (resulting in zero reproductive success from that brood) might also cause him to re-evaluate that site's value when choosing nesting sites the next year.

High levels of spawning site fidelity have been reported for several fish species including Lingcod (*Ophiodon elongatus*), with some males using the exact same nest site from year to year (King and Withler 2005). Nest site fidelity was first reported for a centrarchid (the Smallmouth Bass) in Lake Opeongo, Ontario (Ridgway 1989; Ridgway et al. 1991). Subsequent genetic analyses of offspring from that study by Gross and Kapuscinski (1997) confirmed that level of fidelity. A study on Smallmouth Bass in Miller's Lake, Ontario found that the majority of males there created nests within 20 m of their previous nesting site (Barthel et al. 2008). Similarly, studies on Florida Bass *M. floridanus* introduced into a tropical reservoir in Puerto Rico found that males returned annually to the same spawning areas, with many males returning to the exact same nest over successive years (Waters and Noble 2004). At this time, however, there have been no reports as to whether or not catch-and-release angling impacts nest site fidelity across years. In the nest-guarding Smallmouth Bass *Micropterus dolomieu* external factors such as nest depredation and angling pressure resulted in increased nest abandonment by the guarding male (Philipp et al. 1997; Suski et al. 2003; Suski and Philipp 2004; Hanson et al. 2007; Steinhart et al. 2008). From the standpoint of expected future fitness, a nest-guarding fish that abandoned a nest during one reproductive season should be less likely to return to that same site during subsequent spawning seasons. Alternatively, for a fish that was successful in raising its brood during a given season, it would be expected to choose the same site in successive years (Warner 1988). These expectations, however, have not yet been formally evaluated.

As water temperatures rise above 15 °C during spring, Largemouth Bass move into the littoral zone to prepare nests and spawn, (MacCrimmon and Robbins 1975 and reviewed in Warren 2009). Following successful spawning, males provide sole parental care that involves fanning the eggs and guarding the brood against predators (Brown 1985), and that parental care can last up to five weeks as the brood develops (Cooke et al. 2006). A parental male Largemouth Bass, shortly after its brood becomes free-swimming, escorts the brood away from the nest, presumably to increase brood foraging options and to avoid predation, presumably leading to greater reproductive success (Cooke et al. 2006). Because of this parental/brood movement shortly after the brood become free swimming, researchers have considered a parental male Largemouth Bass successful at that stage (Philipp et al. 1997; Suski et al. 2003). Before the broods can become independent of their fathers, however, predator avoidance behaviors must develop in the young (Brown 1984). A parental male is truly "successful" for that reproductive season only after that level of independence is reached (Brown 1984). If a male abandons the brood before then, the brood will fail, and the reproductive event would be classified as "unsuccessful".

Although inter-annual nest site fidelity in Smallmouth Bass is positively associated with reproductive success (see Ridgway 1989; Ridgway et al. 1991; Barthel et al. 2008), the extent to which this association exists in Largemouth Bass is uncertain. Furthermore, because angled nesting males are more likely to abandon their nests, especially in the face of high levels of brood predation, angling during the spawning season has been linked to decreases in reproductive success (Philipp et al. 1997; Zuckerman et al. 2014; Stein and Philipp 2015). Here we report an unplanned set of observations made during two separate experiments that allows for an assessment of nest site fidelity in an angled Largemouth Bass population. In one experiment nesting males were angled only once during the spawning season versus another experiment in which nesting males were angled multiple times during the spawning season.

Methods

All manipulations and observations were undertaken in Long Lake, a closed access, natural lake of approximately 70 ha, located on the property of the Queen's University Biological Station, near Chaffey's Lock, Ontario (44 deg 30.6 min N, 76 deg 24.3 min W). During 15 years of monitoring Largemouth Bass spawning in Long Lake, we have observed that the entire shoreline of Long Lake is suitable nesting habitat for Largemouth Bass, i.e., shallow, solid substrate with substantial levels of woody debris and other natural structure. The lake is extremely clear, as well as being high sided and heavily wooded, affording it fairly substantial protection from wind effects. In addition, no rain events have ever been observed to cause any kind of noticeable increase in turbidity. Although we have never attempted any type of population estimate, we have never observed even minor fish kills over the last 20 years. For the nine spawning seasons since 1998 in which nesting bass surveys have been conducted in Long Lake, the total number of nesting male Largemouth Bass in the lake ranged from 52–73 with similar size distributions for nesting males across years. This number of nesting males, however, represents some unknown number (but likely a small percentage) of mature males in the lake, only some unknown percentage of which attempt to spawn in any given year. All of these observations suggest that the Long Lake Largemouth Bass population has been stable throughout its recent history. Similarly, we have not observed any obvious changes in the population of brood predators, which is predominantly Bluegill, *Lepomis macrochirus*, but also contains low numbers of Yellow Perch, *Perca flavescens*, and Rock Bass, *Ambloplites rupestris*. Concurrent studies on spawning Bluegill activity indicated no major shifts in population size structure or abundance of this major brood predator across the study periods (DPP personal observations).

We quantified nest site fidelity as the relative distance between an individual male Largemouth Bass' nests in each of two successive years, under two different angling treatments implemented as part of two separate studies conducted in 2004–05 and 2014–15. In the first year of both treatments (i.e., 2004 and 2014, respectively), snorkel surveys of the entire shoreline (approximately 4.2 km) were conducted in May throughout the spawning season to locate nesting Largemouth Bass (and see Philipp et al. 1997; Suski and Philipp 2004). The entire littoral zone of the lake was surveyed every 2–3 days throughout the 5–7 week reproductive season by two snorkelers, a sampling effort previously used to ensure a complete census of all nests within the specified area (e.g., Philipp et al. 1997; Kubacki et al. 2002; Suski et al. 2003). The extremely clear water (10 m visibility) coupled with the fairly narrow littoral zone made a total nest census in Long Lake easier to accomplish than any other study lake. In fact, by assessing the age of the eggs/larvae in each nest at the time of first observation, we determined less than 2% of the nests in the lake were "missed" by the first snorkel pass, and none were missed after two passes. Because each nesting Largemouth Bass is observed guarding its brood approximately 5–8 times during a given spawning season, we feel confident that we monitored all nesting Largemouth Bass during the study. All Largemouth Bass nests were marked with a numbered tile, with the nest locations recorded on a detailed map of Long Lake, and the egg/larval stage, mating success (number of eggs in the brood, using a visual score of 1–5; Kubacki 1992, Stein and Philipp 2015), and nest depth recorded. Only males with nests having an egg score of 2–5 and with eggs < 3 d old that had not started to hatch were used in this study. Subsequently that same day, the guarding males were angled from a boat, measured for total length (TL to the nearest mm), and a passive integrated transponder (PIT tags, Destron Fearing, South St. Paul, MN, USA) implanted in the peritoneal cavity of each angled male bass using a hypodermic needle. Males were then released back onto their nest, less than 30–60 sec after capture. The tenure of parental care (4–5 weeks) was monitored throughout the rest of the reproductive season by snorkelers to determine for each male whether or not it was successful at raising its brood to independence. During the second year of each treatment (i.e., 2005 and 2015, respectively) nesting males were located via snorkeling surveys, their nests marked and mapped as before, and then males were angled just once again to determine the identity of these males by reading the PIT tags implanted during the previous year. All angling was done using spinning equipment and one of three lure types, 4.5 inch floating silver Rapala, 1/8 oz jig with a white twister grub, 6 inch Texas-rigged black worm. None of the angled fish used in this experiment was hooked deeply, nor did any suffer wounds that bled.

For the 2004 treatment, the nesting males were angled multiple times, resulting in multiple recaptures (up to six for some males, extending for 12 days after the initial capture) of each nesting male during the nesting period. Starting when it was first discovered, i.e., when its brood was at the egg stage, each male was angled every other day until it had abandoned its nest, which ranged from after the first capture for some up to after the sixth capture for a few. Almost every test male, if it was still guarding its brood, was caught on each of these angling days. There were two males, however, that anglers could not catch after their second capture. These two males were the only ones that successfully raised broods to the free-swimming fry stage; all others abandoned their broods prematurely. For the 2014 treatment, however, each nesting male was angled and captured only once during the nesting period. After the first years of both treatments, the nest tags were left over summer and winter for comparison with new nest locations during year two.

In the second year of both treatments (2005 and 2015), nesting males were angled only once during the spawning season, and all adult Largemouth Bass were checked for a PIT tag. If the captured male had been tagged the previous year, its location was marked on a detailed map of the lake. The distance between first-year nest site and second year nest site for each of the test Largemouth Bass was determined as the straight-line distance between the two nest sites. This was accomplished in one of two ways. For nests sites that were less than 100 m apart, it was determined by directly measuring the distance between the nest tags from year one and two for each test bass from a boat using measuring lines. For more distant nest sites, they were calculated from map locations recorded on the nesting site map over the two successive years using google earth distance measurements. Accuracy for the first technique was to within +/− 1 m for nests less than 25 m apart and to within +/− 5 m for nests that were between 25 m and 100 m apart. Distances for the second technique (Google Earth) had +/− 10m accuracy. Differences in the distances between first year and second year nest sites for both treatments were compared using a Mann–Whitney test due to the non-normal distribution of the data.

Results

In 2004, 36 nesting males were repeatedly angled until either the male abandoned its nest or the male could no longer be captured. Two males (5.6%) that successfully raised their brood to independence could only be captured twice and did not abandon their nests, while the remaining 34 males (94.4%) all abandoned their nests prematurely. Of those 34 males, 11 abandoned their nests after two recaptures, 12 after three recaptures, seven after four recaptures, two after five recaptures and the remaining two after six recaptures. In 2014, 60 nesting males were angled only once, and 58 (96.7%) successfully raised broods.

Of the 36 nesting males captured multiple times in 2004, 19 were captured again off nests in 2005 and determined via PIT Tag to all have been unsuccessful nesters in 2004; 17 of those 19 males (89.5%) were successful at raising their broods during the second year (2005) when they were angled only once for individual PIT tag identification. For the single angling treatment in 2014, 32 of 60 successful nesting males captured in 2014 were re-captured off nests in 2015, and 27 of those 32 males (84.3%) were successful at raising their broods during the second year (2015).

During the single angling treatment of 2014–2015, nesting males ($n = 32$) were significantly more likely ($U = 84.0$, $P < 0.001$) to re-nest near their previous year's nest location ($\bar{x}$ = 13.9 m ± 4.9 SE) than the nesting males ($n = 19$) experiencing the multiple angling treatment of 2004–2005 ($\bar{x}$ = 111.6 m ± 31.6 SE). More specifically, in 2015 59% of males used nesting sites that were within 5 m of their previous year's sites, and another 28% of males were within 10 m, total = 87% (Fig. 1). In 2005, however, only 11% of males used nesting sites that were within 5 m of their previous year's sites, and another 16% of males were within 10 m, total = 27% (Fig. 1).

Discussion

First, we want to re-iterate that this report arose from data that were collected as part of two different, unrelated experiments. As such, we admit that the design is imperfect in that the treatments were applied in different years. We want to stress, however, that nothing about the population of Largemouth Bass or the fish community in general in Long Lake as a whole changed noticeably

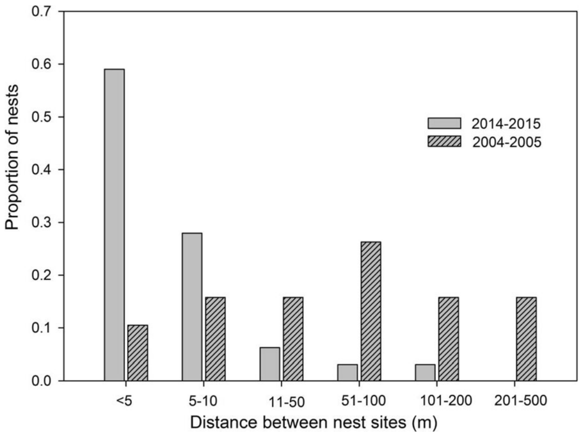

Fig. 1 The proportion of bass nests in 2015 and 2005 that were within 5, 10, 50, 100, 200, and 500 meters from the previous year's nest, after males had been angled and captured once during the 2014 nesting period (with high nesting success) and multiple times during the 2004 nesting period (with low nesting success) (U = 84.0, $P < 0.001$)

from 2004 to 2015. Indeed, the lake is used solely for research related to monitoring the long-term reproductive success of Largemouth Bass with no fishing pressure from the general public. In addition there were no environmental or physical conditions within the lake that obviously varied between 2004–2005 and 2014–2015. Finally, the sizes of the nesting Largemouth Bass in 2004 (TL = 373 mm, SE = 31.9 mm; range = 325–433 mm) was very similar to those of the nesting Largemouth Bass in 2014 (TL = 375 mm, SE = 28.8 mm; range = 315–441 mm), as was the mating success in the two years (egg score = 3.3, SE = 0.7 in 2004 and egg score = 3.4, SE = 0.7 in 2014). As a result, we feel that our observation that nest site fidelity in this Largemouth Bass population was less following a year of heavy angling on nesting males than following a year in which nesting males were angled only once warrants circulation to the research, angling, and management communities.

Our observation of a very high level of nest site fidelity (87% nesting within 10m of the previous year's site) for male Largemouth Bass that were angled only once during the previous year is consistent with what has been reported for Florida Bass introduced into a tropical reservoir in Puerto Rico (Waters and Noble 2004). We observed a much lower level of nest site fidelity, however, for male Largemouth Bass following a spawning season in which nesting males were angled multiple times. Only 27% of these males nested within 10 m of their previous year's nest, with the majority of fish nesting more than 50 m away. Although there is little research on this topic in fish, previous research on birds has revealed that disturbance during nesting does reduce nest site fidelity. Blackmer et al. (2004) studied Leach's Storm-Petrels (*Oceanodroma leucorhoa*) during parental care and reported that both weekly and daily investigator disturbance during incubation reduced hatching success and subsequent nest-site fidelity of the parents.

The high rates of multiple re-capture during the 2004 spawning season resulted in over 90% of the nesting males prematurely abandoning their nests. Increased brood predation in Largemouth Bass has been attributed to angling during the nesting season (Stein and Philipp 2015); i.e., as males are temporarily removed from their nest, predators such as Bluegill can prey upon an unguarded nest. This angling-induced loss of brood can lead to premature abandonment of the nest by the parental male (Zuckerman et al. 2014), particularly when there is a possibility of additional mating opportunities (Gross 2005). In addition, because males suffer a reduction in locomotory activity for up to 24 hours post-angling (Cooke et al. 2000), angling may also affect a male's parental care ability after the angling event. The potential for premature nest abandonment provides the basis for a 'lose-move' decision for choosing next year's nesting site (Switzer 1993), and there is evidence that formative experiences can be retained over time by fish (Kieffer and Colgan 1992; Laland et al. 2003; Brown et al. 2011).

Even though the treatments were not replicated across multiple years or manipulated within a single year together (because this *post hoc* observation was not a goal of the studies generating the data), the magnitude of differences in the level of nest site fidelity between reproductively successful and unsuccessful groups warrants consideration of this observation. Even though this experiment required reasonably large closed-access populations of Largemouth Bass in wild settings and two years of study to get each dataset, we encourage other researchers to test the hypothesis generated by our observations; i.e., that angling nesting bass (or other forms of anthropogenic disturbance) decreases subsequent nest site fidelity via the facilitation of brood predation that reduces reproductive success (Stein and Philipp 2015) or even causes premature abandonment of the brood (Zuckerman et al. 2014). This finding may indicate that angling could cause male bass to abandon historically successful nest sites in favor of new, untested ones, a decision that may have long-term implications for reproductive success rates in Largemouth Bass.

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