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RESEARCH ARTICLE

Do protected areas mitigate the effects of fisheries-induced evolution on parental care behaviour of a teleost fish?

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Abstract

1. While the use of aquatic protected areas that exclude angling might be considered an evolutionarily enlightened management approach to dealing with fisheries-induced evolution (FIE), there is little empirical data on the effectiveness of this approach at maintaining the diversity of phenotypic traits within protected areas.
2. In species with paternal care, including largemouth bass (*Micropterus salmoides*), active nest-guarding and aggression towards potential brood predators by males may render these individuals particularly vulnerable to capture by angling because of increased propensity to attack fishing lures/bait near their nests. Relative levels of aggression by these males during the parental care period correlates with their vulnerability to angling year round. Selective removal of more aggressive individuals by anglers should drive population-average phenotypes towards lower levels of aggression.
3. To assess the effectiveness of protected areas at mitigating FIE, the parental care behaviours of wild, free-swimming male bass were compared during the early nesting period for bass within and outside protected areas in a lake in eastern Ontario. Nesting males within long-standing aquatic protected areas closed to fishing for >70 years were more aggressive towards bluegill sunfish (*Lepomis macrochirus*), a potential nest predator, and patrolled larger areas around their nests compared with bass outside of sanctuaries. Males within protected areas were also more likely to strike at artificial fishing lures and were more prone to capture during angling events.
4. Collectively, the findings suggest that the establishment of protected areas may promote phenotypic diversity such as more attentive and vigorous parental care, relative to areas open to angling. The extent to which this phenomenon occurs in other species and systems is likely to depend on the reproductive strategies of fish and their spatial ecology compared with protected area boundaries, and habitat quality within protected areas.

KEYWORDS

behaviour, fish, fishing, lake, protected areas

1 | INTRODUCTION

The selective pressures imposed on wild fish populations by fisheries harvest (commercial, artisanal and recreational) have resulted in fisheries-induced evolution (FIE) in exploited species (Heino & Godø, 2002). Significant changes due to FIE have been observed over periods as short as one generation (Philipp et al., 2009) up to the scale of decades (Law, 2007). Selection on life-history characteristics, such as earlier maturation at smaller body sizes, have received extensive study as these factors directly decrease fisheries yields (Kuparinen & Merilä, 2007). There has been less attention devoted to FIE effects on behavioural traits and their associated physiological processes (Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008), with these characteristics influencing the vulnerability of target species to different types of fishing gear (Wilson, Binder, McGrath, Cooke, & Godin, 2011). Whole-lake experiments with passive fishing gear (gillnets) demonstrate selection against faster-growing phenotypes as a result of their increased vulnerability to capture stemming from their greater levels of activity and boldness (Biro & Post, 2008). In largemouth bass (*Micropterus salmoides*), artificial selection for phenotypes that have high or low vulnerability to capture by recreational angling indicated that angling vulnerability is a heritable trait (Philipp et al., 2009). Certain behavioural phenotypes associated with high baseline activity levels, elevated boldness and aggression (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011) may be selected against in populations exposed to angling pressure (Alós, Palmer, & Arlinghaus, 2012).

Fisheries-induced evolution selecting against boldness and aggression may disproportionately remove individuals with the greatest fitness potential that in part results from their tendency to exhibit the highest levels of parental care (Sutter et al., 2012). Parental care can augment the reproductive output of an individual by increasing the survival rate of offspring through nest tending and/or aggression against potential nest predators (Clutton-Brock, 1991). In teleost fishes, parental care is often undertaken by males (Blumer, 1979; Breder, 1936; Smith & Wootton, 1995) with the level of care positively correlated with the number of eggs, past reproductive success and the likelihood of subsequent mating opportunities (Gross, 2005) as predicted by the ‘asset protection principle’ (Clark, 1994). Male black bass (*Micropterus* spp), in particular, demonstrate positive relationships between levels of aggression towards nest predators and the number of eggs within nests (Suski & Philipp, 2004). These relatively high levels of aggression may render such species particularly vulnerable to removal should they mistake angling gear for potential nest predators (Philipp, Toline, Kubacki, Philipp, & Phelan, 1997). Relative levels of aggression by nest-guarding bass persist beyond the reproductive period and are correlated with their vulnerability to angling during open seasons when anglers are legally allowed to target bass (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007). Fisheries-induced evolution (FIE) will occur in populations exposed to catch-and-harvest fisheries but also in catch-and-release fisheries because of post-release mortality (reviewed in Siepker, Ostrand, Cooke, Philipp, & Wahl, 2007). Temporary removal of nest-guarding bass can also be a mechanism for FIE, as parental absence may lead to brood reduction through predation and increased rates of nest abandonment (Stein & Philipp, 2015). Ultimately, reduced reproductive success of fished bass may decrease the frequencies of phenotypes most associated with aggression, parental care, and angling vulnerability (Philipp et al., 2015; Stein & Philipp, 2015). Previous studies of FIE-mediated vulnerability to angling show that fish in unexploited lakes are more vulnerable to capture than fish in heavily fished lakes (Philipp et al., 2015) and have higher metabolic rates (Hessenauer et al., 2015), although these observations may be confounded by differences in the characteristics of lakes or biological factors between populations.

To mitigate the effects of FIE on species of interest, there have been efforts to develop evolutionarily enlightened management strategies (*sensu* Ashley et al., 2003), including designating particular areas within the home range of a species as off-limits for all forms of harvest. Protected areas or sanctuaries have been widely implemented in both marine (Agardy, 1994; Sciberras et al., 2015) and freshwater (Saunders, Meeuwig, & Vincent, 2002; Suski & Cooke, 2007) systems. In lakes, protected areas enable direct comparisons of the effects of fishing pressure on the characteristics of protected vs. exploited sub-populations (Cooke & Cowx, 2006). This study builds on earlier inter-lake data by focusing on fish inside and outside protected areas within a single water body. To assess the effects of fishing pressure on bass from inside and outside of protected areas, bass inside the sanctuary should represent a relatively distinct sub-population with high site fidelity. On Long Lake, (Elgin, ON, Canada), 87% of males nested within 10 m of the site they used in the previous year (Twardek et al., in press). These findings are consistent with the site fidelity of largemouth bass in tropical reservoirs, where 78% of males nested within 50 m of their site the year before (Waters & Noble, 2004). A telemetry study during the open fishing season (there is a closed season from December 15 to the third Saturday in June annually to protect spawning bass throughout the entire lake) on largemouth bass tagged within a fish sanctuary in Lake Opinicon, the study system, indicated that sanctuary males occupying areas with high habitat complexity had 91% of detections fall within the boundaries of the sanctuary (DeMille, 2010). In addition, none of the non-sanctuary bass moved into the sanctuary during the monitoring period (DeMille, 2010). Fry dispersal out of the sanctuary could also reduce the genetic distinctiveness of the sanctuary fish, although given typical dispersal distances (mean of 302 m and all <515 m in a 26 ha lake; Hessenauer, Bremigan, & Scribner, 2012) and the size of each sanctuary (1 km in length), the majority of fry should remain within sanctuary boundaries after dispersal. These studies suggest that bass found inside and outside protected areas can be treated as somewhat demographically distinct.

Largemouth bass are an ideal model to use for this research for several reasons. First, they are often apex predators in freshwater lentic systems, structuring lacustrine fish communities (Drenner et al., 2002; Turner & Mittelbach, 1990). Removal of largemouth bass from a fish assemblage can result in rapid and dramatic changes in food web structure by increasing the abundance of planktivorous fish (Mittelbach, Turner, Hall, Rettig, & Osenberg, 1995). Largemouth bass are also regarded as being relevant indicators of environmental change in lentic ecosystems given that changes in their density can lead to regime shifts (Carpenter et al., 2011). This species is renowned as the most popular sportfish in North America (Quinn & Paukert, 2009) but also faces pressures from habitat alteration (Ahrenstorff, Sass, & Helmus, 2009). Given their value as a sportfish but also their important role in freshwater ecosystems, they are of great interest from both fisheries management and conservation perspectives.

The present study explores how differential angling pressure may influence the evolution of fish behaviour over ecological timescales. The hypothesis is tested that recreational angling has resulted in differences in parental care behaviour of male bass protected from angling within fish sanctuaries relative to bass outside these areas. It is predicted that bass from within exploited areas will demonstrate lower levels of nest attentiveness and aggression towards potential nest predators than bass from within fish sanctuaries, and that fish outside the protected areas will also be less likely to be captured during controlled angling experiments. Observed differences would comprise indirect evidence that protected areas have been effective at maintaining phenotypic diversity and served as an evolutionarily enlightened management strategy (Ashley et al., 2003), even if that was not the intent when they were first designated.

2 | METHODS

2.1 | Study site and species

All work was conducted in Lake Opinicon at the Queen's University Biological Station in Elgin, ON (N 44° 33′ 56.0″, W76° 19′ 23.6″; Figure 1) between 3 and 6 May 2015. Opinicon is mesotrophic with a mean depth of ~2.8 m and an area of ~780 ha (Agbeti, Kingston, Smol, & Watters, 1997) with two long-established fish sanctuaries where angling is prohibited year round. These were established in 1939 (Murphy Bay fish sanctuary, 83 ha) and 1945 (Darlings Bay fish sanctuary, 14.2 ha) by the Ontario Ministry of Natural Resources and Forestry (OMNRF, formerly Lands and Forests) specifically for the conservation of largemouth bass. Although the sanctuaries were initially implemented as a means of maintaining quality of the recreational fishery, over time it has had the potential to play a broader role in conservation by providing unaltered habitat for protected species. These sanctuaries are located approximately 6 km apart on the east (Murphy Bay) and west (Darlings Bay) ends of the lake, and both contain ideal largemouth bass nesting habitat. Both sanctuaries are located in 'drowned land' areas, which contain many immersed stumps and fallen tree trunks resulting from flooding from construction of the Rideau Canal during the late 1820s (Karst & Smol, 2000). Lake Opinicon has a relatively high burden of nest predators (Gravel & Cooke, 2009) composed primarily of bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), and rock bass (*Ambloplites rupestris*).

Sixty-eight free-swimming, nesting male largemouth bass (all >23 cm total length) were assayed for parental care behaviour: 17 fish were sampled in each of the two sanctuary areas and 34 were sampled outside the sanctuaries. Only males from nests with similar habitat characteristics were included (shallow areas <1 m depth, coarse woody structure, and high vegetation densities; Ahrenstorff et al., 2009; DeMille, 2010) to minimize any habitat-mediated differences in behaviour. Although behaviour in fishes is strongly influenced by environmental conditions, including temperature (Lemons & Crawshaw, 1985) and predation pressure (Cooke, Weatherhead, Wahl, & Philipp, 2008), these factors did not differ significantly between the two sanctuaries, between the non-sanctuary areas, or between the sanctuary and non-sanctuary areas (all $P > 0.05$).

2.2 | Experimental protocol

Snorkelling surveys were conducted to locate nesting males guarding newly spawned eggs (< 3 days old). The size of nesting males (total length) and their relative nesting success (ordinal ranking of the number of eggs in the nest from 1 (low) to 5 (high), after Philipp et al., 1997; Stein & Philipp, 2015) were estimated through visual assessments. Egg abundance in nests is positively associated with levels of aggression towards potential nest predators (Suski & Philipp, 2004) and nests with fewer eggs tend to have higher levels of abandonment (Zuckerman, Philipp, & Suski, 2014), so only males with mating success scores ≥3 were observed. Parental behaviour of the nesting males was assessed through four different assays by a snorkeller and all snorkellers ($N = 4$) received identical training in assessment methods before beginning the study (Stein, Claussen, Cooke, & Philipp, 2014).

The following three behavioural tests were completed before assessing angling vulnerability. First, the nest attentiveness of bass was observed for 3 min, with nest attentiveness considered as the proportion of time the male spent on the nest protecting its brood out of the entire 3 min. The fish was assigned a score of 0 when it was more than 1 m from the nest or a score of 1 when it was within 1 m of the nest at 20 s intervals (O'Connor, Gilmour, Arlinghaus, Van Der Kraak, & Cooke, 2009). The level of nest attentiveness was determined by dividing the total attentiveness score by the number of observations made (9). During this 3-min period the number of potential predators (bluegill, pumpkinseed, rock bass) that came within 1 m of the nest was recorded and used as a measure of ambient predator density. The male was then presented with a model brood

FIGURE 1 Map of Lake Opinicon. Solid lines indicate the boundaries for (A) Darling's Bay and (B) Murphy Bay fish sanctuaries

predator consisting of a resin-coated photograph of a bluegill sunfish mounted on a plexiglass backing attached to a 1.5 m dowelling rod (Coleman, Gross, & Sargent, 1985; Suski, Svec, Ludden, Phelan, & Philipp, 2003). The model was presented at distances of 2 m, 1 m, 0.5 m and on the nest (0 m) for periods of 10 s each or until the nesting male 'rushed' (male swam quickly towards the model), 'struck' (male made physical contact with the model) or 'yawned' (male opened his mouth and flared his branchiostegal membranes) at the model (after O'Connor et al., 2009; Suski & Philipp, 2004). The furthest position of the model from the nest that elicited one of these behaviours by the male bass was recorded as the response distance. Third, a glass jar containing a small live bluegill was placed directly onto the nest for a 1-min period, during which the cumulative number of the three aggressive behaviours directed at the bluegill was recorded as the number of aggressive attempts.

After completion of the three behavioural assays, the nesting males were allowed to recover for 10 min before testing their vulnerability to angling. A fishing boat was positioned using an electric trolling motor at a distance of ~10 m from the nest to avoid disturbing the focal fish. Snorkellers remained a minimum distance of 5 m away during angling, and performed nest-guarding duties until the male was released back onto its nest. Anglers presented each male with five casts each of a 10 cm white stick bait (Storm®), followed by a 10 cm green power worm (Berkley®) and then a 10 cm white tube (Berkley®). The order of lure presentation was identical for all males, and three different lures were used to increase the likelihood of eliciting a response from a nesting male. Consistency among anglers was achieved by including only those casts entering the water within 1 m of the nest, with all other casts being disqualified (<10%). If the nesting male demonstrated an anti-nest predator response by attacking or ingesting the lure, the angler attempted to hook and land the fish. Each cast was given a score as follows: no response (score of 0), male made contact with the lure (score of 1), or male was hooked (score of 2). Once the male was hooked or landed the lure presentation ceased, and all landed fish were measured (total length, TL), and released immediately onto their nest. The mean total length of fish both inside and outside the sanctuaries was approximately 38 cm (15 in).

2.3 | Statistical analyses

To justify the pooling of the two sanctuary samples into one group, and two non-sanctuary fish samples into another, a MANOVA was performed for the various behavioural responses. No significant differences were found in the multivariate behavioural responses of fish between sanctuary areas ($P > 0.05$) or between non-sanctuary areas ($P > 0.05$), so they were pooled into two distinct groups for comparison (sanctuary vs. non-sanctuary fish). The behavioural responses of fish inside and outside sanctuaries were compared as generalized linear models with distributions suited to the types of data: binomial for discrete events (nest attentiveness and strikes per cast), Poisson for count data with low mean (number of aggressive attempts) and normal for categorical data (response distance to the bluegill model). In all models, ambient predator density counts and body size were included as covariates. Significance was considered at $\alpha = 0.05$. R v2.15.1 (R Core Team, 2015) was used for the analyses and figures were generated with SigmaPlot v11.0 (Systat Software, Inc., San Jose CA).

3 | RESULTS

Full statistical results are presented in Table 1. Nest attentiveness was significantly more common in males outside the sanctuaries compared with those inside ($F_{1, 66} = 9.62$, $P = 0.0028$; Figure 2a). Nesting males within the sanctuaries did not show a significant difference in response distance to the model predator compared with males outside the sanctuaries ($F_{1, 66} = 1.10$, $P = 0.30$; Figure 2b). Males within sanctuaries demonstrated significantly greater numbers of aggressive attempts than their counterparts outside the sanctuaries when presented with a live nest intruder ($F_{1, 66} = 4.36$, $P = 0.041$; Figure 2c). The sanctuary males had significantly greater numbers of strikes per cast than non-sanctuary males ($F_{1, 66} = 10.17$, $P = 0.002$; Figure 2d), corresponding to 44% of the males inside sanctuaries being caught during angling events vs. 21% outside the sanctuaries. No significant relationship was found between any of the behavioural measures and the number of nest predators present (all $P > 0.05$), suggesting that these behavioural differences are the result of angling and not local variation in ambient predation pressure. In addition, no significant relationship was found between any of the behavioural measures and the size of the fish (all $P > 0.05$), indicating that these behavioural differences are not size-dependent across the range of adult sizes studied here. There was no significant difference in the size of fish inside vs. outside the sanctuaries ($P > 0.05$).

4 | DISCUSSION

Male largemouth bass provide parental care to their offspring, guarding them from predators during the early stages of development (Breder, 1936). To protect against brood predators such as bluegill and pumpkinseed, males act aggressively by yawning, rushing and striking at intruders. Angling selectively targets and removes the most

TABLE 1 Generalized linear model comparison of behavioural responses of nest-guarding male largemouth bass (*Micropterus salmoides*) inside and outside fish sanctuaries (location) with male body size (total length, inches) and ambient predator density as linear covariates

	Location			Body size			Predator density			
Response	F	df	P	F	df	P	F	df	P	Distribution
Nest attentiveness	9.62	1, 66	0.0028	2.29	1, 65	0.14	0.432	1, 65	0.51	binomial
Response distance	1.10	1, 66	0.30	0.12	1, 65	0.73	1.88	1, 65	0.17	normal
No. aggressive attempts	4.36	1, 66	0.041	1.93	1, 65	0.17	2.70	1, 65	0.11	Poisson
No. strikes per cast	10.17	1, 66	0.0022	2.91	1, 65	0.092	0.0066	1, 65	0.94	binomial

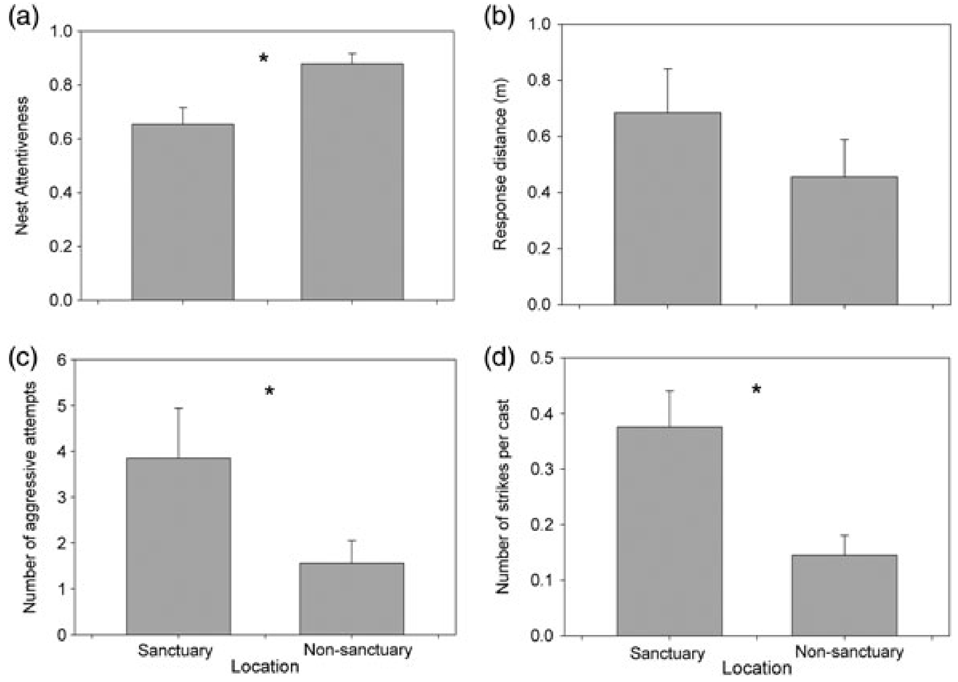

FIGURE 2 Mean (+ SE) values of observed (a) proportion of time devoted to nest attentiveness; (b) response distances to a model brood predator; (c) number of aggressive attempts towards a live intruding brood predator; and (d) number of strikes per cast for three different lures presented in standardized order demonstrated by male largemouth bass inside and outside of fishing sanctuaries. Asterisks (*) denote statistically significant differences between treatments ($P < 0.05$)

aggressive fish from populations (Sutter et al., 2012), and even catch-and-release angling can result in mortalities from injury and physiological impairment from capture and handling (reviewed in Siepker et al., 2007). Over time this may lead to FIE and less aggressive populations with correspondingly weaker or less effective parental care (Philipp et al., 2015). One means to diminish the potential effects of FIE is to designate protected areas that restrict recreational angling, which should limit the selective removal (through harvest or angling-associated mortality) of those individuals providing the greatest levels of parental care.

The observed behaviours of nesting largemouth bass inside and outside protected areas are consistent with the prediction that males in protected areas provide greater levels of parental care by elevated aggression towards captive nest predators compared with their counterparts subject to angling pressure. Furthermore, these traits are positively associated with increased susceptibility to angling as sanctuary bass performed more frequent strikes towards artificial lures, which in turn can result in increased catches attributable to aggression (44% caught in the sanctuary vs. 21% caught outside the sanctuary). Aggression is positively correlated with metabolic rate in bass (Cooke et al., 2007; Redpath et al., 2010; Sutter et al., 2012), which has been found to be selected against in heavily exploited populations (Hessenauer et al., 2015). The relationship between aggression and metabolic rate provides a physiological explanation for the observed differences in behaviour. The present finding suggesting that angling selects against the trait of nest-guarding aggression is consistent with what has been observed between lakes with different levels of fishing intensity (Philipp et al., 2015); however, the within-lake comparison assesses the potential for protected areas to mitigate this change. In Lake Opinicon, telemetry data supports some level of population distinctiveness (DeMille, 2010) despite the absence of corroborating genetic evidence. For the observed differences to be attributed to evolution, the selective pressure of recreational fishing would have to outweigh the homogenizing effect of gene flow. Gene flow between the sanctuary and non-sanctuary areas would only reduce the magnitude of the observed differences in parental care behaviour. It could be predicted that complete physical isolation of the sanctuary would only magnify the difference observed between fish in the two areas. Given the consistency of temperature, ambient predator density, habitat, and body size of fish across study areas we suggest that the rather striking differences in behaviour observed are the result of variation in fishing pressure. It should be noted that these findings may alternatively be explained to some extent by phenotypic plasticity, as suggested in two population sub-units of European hake (*Merluccius merluccius*) although those sub-units occupied different habitat types (Hidalgo et al., 2014).

Bass outside sanctuaries demonstrated lower mean numbers of strikes per cast than bass inside sanctuaries. This could be due to the removal of more aggressive individuals or the result of previous exposure to fishing lures, and might therefore represent a learned, experience-based response to avoid these items (Beukema, 1970; Klefoth, Pieterek, & Arlinghaus, 2013; van Poorten & Post, 2005). Although there is little evidence for hook avoidance in largemouth bass, the species has shown some ability to learn in response to an electric shock (although only 12–34% learned by the fourth exposure; Coble, Farabee, & Anderson, 1985). Previous experimental angling studies on the responses of bass towards artificial lures have shown that the capture susceptibility of individuals does not change with increased levels of exposure, although naïve bass seem to strike more readily (Hackney & Linkous, 1978). Continuing work has also indicated that they may not recognize particular lures after periods of one year have elapsed (D. Philipp, unpublished data), suggesting a temporal limit to the memory window of retaining acquired information (Brown et al., 2013). The males fished for outside the protected areas during this study would have had a minimum of 6 months since their last exposure to fishing gear owing to seasonal lake-wide closure from December 15 to the third Saturday in June. Although vulnerability to angling appears to be heritable (Philipp et al., 2009), quantifying the relative contributions of genetics and acquired information to the behavioural responses in largemouth bass requires additional research.

In heavily exploited areas, low vulnerability phenotypes may become more prevalent, which will have repercussions for the quality of the recreational fishery (Alós, Palmer, Trias, Diaz-Gil, & Arlinghaus, 2014). In exploited systems, these low vulnerability males may be less likely to succumb to harvest, suggesting a fitness advantage. However, a consequence of removing the most aggressive fish is a population with weakened parental care (Cooke et al., 2007), leading to decreased survival of age-0 offspring and potentially diminished adult recruitment (Parkos, Wahl, & Philipp, 2013; Sutter et al., 2012; but see Jackson, Einhouse, Van De Valk, & Brooking, 2015). The reduction in angling vulnerability of bass from within and outside protected areas is consistent with findings for catch rates in differentially exploited largemouth bass populations (Philipp et al., 2015). This also has practical implications to inform conservation policies as this study has demonstrated that more vulnerable males have greater levels of parental care aggression.

Male bass outside the sanctuaries spent more time on their nests than males inside the sanctuaries. One explanation for this could be that the more aggressive nesting males in the sanctuaries spend more time away from the nest chasing off brood predators and patrolling their nest site compared with those outside sanctuaries. Departing from the nest to chase predators is common in systems where predation levels are high (Cooke et al., 2008). Under this scenario there could be a tradeoff between high activity/boldness and nest attentiveness (Alós et al., 2012; Härkönen, Hyvärinen, Paappanen, & Vainikka, 2014; Klefoth et al., 2013). The higher nest attentiveness demonstrated by non-sanctuary males supports the idea that angling selects for less active/bold phenotypes with such males spending more time on the nest and less time engaging lures/brood predators around nest sites. The observation that nest attentiveness is greater for males outside the sanctuaries may show that not all FIE selects against adaptive traits, as is generally assumed (Kuparinen & Merilä, 2007). However, effective parental care involves a combination of behaviours including those related to vigilance, patrolling, tending and predator engagement. Failing to engage predators from afar or immediately in the nest would be a poor strategy for brood defence in lakes with high predator burdens, including Lake Opinicon (Gravel & Cooke, 2009).

Fisheries-induced evolution has been shown to act on a variety of traits including those related to physiology, life history, and behaviour (reviewed in Heino & Godø, 2002). Protected areas appear to be preserving phenotypic diversity in parental care behaviours which may achieve greater recruitment success at the population level (Sutter et al., 2012). Given the role of largemouth bass in structuring lentic ecosystems, strategies that ensure their persistence and protect a broad range of phenotypes would benefit not just bass populations and the fishery, but broader aquatic ecosystems. The extent that these findings may be applied to other species is dependent on their reproductive behavioural strategies and their spatial ecology relative to protected area boundaries. To increase the confidence that these findings are attributable to FIE, microgeographic population structure could be assessed for fish within and outside the sanctuaries. Additional work is needed to understand if simply limiting harvest (i.e. catch-and-release only) would be sufficient to prevent changes in behaviour, particularly because this would also require that released fish survive an angling event. Moreover, fishing during the parental care period would presumably need to be restricted to ensure that males engaged in parental care were not temporarily removed from nests by anglers, leading to reductions in brood size and subsequent abandonment (Philipp et al., 1997). This study expands the toolbox for conservation and resource management agencies in developing and refining evolutionarily enlightened management strategies.

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