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ARTICLE

Does capture method or the presence of aquatic protected areas influence the selective harvest of behavioural types in largemouth bass?

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Abstract: Selectively removing fish based on particular traits, such as body size, may shift trait abundance in the remaining population, resulting in a phenomenon called fisheries-induced evolution. Recently, there is growing interest in evaluating the effects of fisheries-induced evolution on fish behaviour. Aquatic protected areas (APAs) have been designated in some habitats in efforts to prohibit harvesting and maintain natural ranges of phenotypic variation for impacted species. Here, we attempted to test whether APAs that prohibit all forms of fishing have an evolutionary influence on adult largemouth bass (*Micropterus salmoides*) behaviour by investigating the relationship between capture method and behavioural type. Fish, caught via active (angling) and passive (hoop net) capture techniques in both protected (70+ year old APAs in eastern Ontario) and adjacent nonprotected areas, were subjected to standard tests of boldness (refuge emergence, general activity, and flight-initiation-distance). A behavioural syndrome characterized by consistent within-individual variation and correlation of boldness behaviours (activity and refuge emergence) was present. Our results provide evidence that APAs may promote behavioural diversification and protect traits selectively targeted by recreational angling.

Résumé : Le retrait sélectif de poissons en fonction de caractères précis, comme la taille du corps, pourrait modifier l'abondance de caractères dans la population restante, entraînant un phénomène dit d'évolution induite par la pêche. Il y a actuellement un intérêt croissant pour l'évaluation des effets de l'évolution induite par la pêche sur le comportement des poissons. Des zones aquatiques protégées (ZAP) ont été désignées dans certains habitats dans des efforts visant à interdire la récolte et maintenir les aires de répartition naturelles de variations phénotypiques pour des espèces touchées. Nous tentons de déterminer si les ZAP où sont interdites toutes formes de pêche ont une influence évolutionnaire sur le comportement d'achigans à grande bouche (*Micropterus salmoides*) adultes en examinant la relation entre la méthode de capture et le type comportemental. Des poissons capturés par des méthodes de pêche active (pêche à la ligne) et passive (verveux) dans des zones protégées (des ZAP établies depuis plus de 70 ans dans l'est de l'Ontario) et non protégées attenantes ont fait l'objet de tests de hardiesse (sortie de refuge, activité générale et distance d'initiation de la fuite). Un syndrome comportemental caractérisé par des variations cohérentes chez un même individu et la corrélation de comportements de hardiesse (activité et sortie de refuge) était présent. Nos résultats fournissent des données qui indiquent que les ZAP pourraient favoriser la diversification comportementale et protéger des caractères sélectivement ciblés par la pêche récréative. [Traduit par la Rédaction]

Introduction

Targeted removal of individuals with desirable phenotypes such as size, morphology, or particular behavioural traits has altered their mean values within exploited populations. Commercial and even large-scale recreational harvesting of fish populations have driven this selective process in both target and bycatch species, leading in many cases to fisheries-induced evolution (FIE) (Allendorf and Hard 2009). Such anthropogenic or artificial selection on traits as a result of harvest in aquatic systems has reduced the frequencies of "desirable" phenotypes and genotypes in many wild fish populations (Biro and Post 2008). While FIE has been recognized in the context of commercial fisheries for some time (e.g., Heino and Godø 2002; Law 2007), comparatively, it is only recent that recreational fisheries have been recognized as important in this context (Cooke et al. 2007; Philipp et al. 2009; Wilson et al. 2011, 2015). In contrast with commercial harvesting where most captured fish are retained, recreational fisheries often involve the voluntary or mandated release of captured fish of particular species. Although retention rates in recreational fisheries approach zero for some species, this can still be substantial, particularly given the often isolated nature of inland fisheries (Cooke et al. 2002*a*; Arlinghaus and Cooke 2009; Brownscombe et al. 2014). Despite the fact that fish survival is an implicit goal of catch-and-release, capture-related injury, stress, and associated

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Table 1. Summary of mean (±SE) behavioural and morphological attributes of largemouth bass (*Micropterus salmoides*) caught inside or outside APAs via angling or hoop net.

Behavioural/ morphological attribute	Outside APA	Inside APA	Angling	Hoop net
Refuge emergence (s)	463.08±26.08	476.73±22.24	449.35±24.57	490.46±23.68
Activity (no. of lines crossed)	30.57±1.96	26.11±2.21	32.02±2.33	24.66±1.74
FID (cm)	30.78±4.64	23.51±4.53	28.51±4.74	25.78±4.48
Total length (mm)	357.45±6.11	364.56±7.17	361.0±7.02	360.94±8.84

post-release mortality could also contribute to FIE (Muoneke and Childress 1994; Cooke et al. 2002*b*). Factors including capture technique (Wilson et al. 2011, 2015), gear type, and angler experience (Dunmall et al. 2001) all have the potential to contribute to the removal of certain phenotypes.

Most studies have focused on the effects of FIE on body size, as fisheries tend to target larger individuals for harvest (e.g., Jennings et al. 1999; Sinclair et al. 2002; Saura et al. 2010; Alós et al. 2014). Targeting larger individuals may ultimately decrease overall body size, age at sexual maturity, and fecundity levels (Heino and Godø 2002; Uusi-Heikkilä et al. 2008). In addition to determining the effects of selective harvesting on morphology and life histories, studying associated changes in animal behaviour has become increasingly prevalent (Biro and Post 2008). Boldness, or the extent to which an individual will adopt risk-prone behaviours, is associated with a suite of fitness-related traits including spatial exploration, foraging innovation, mate selection, sociability, and antipredator behaviours (Wilson et al. 1993, 1994; Réale et al. 2007; Elvidge et al. 2016). In bluegill sunfish (*Lepomis macrochirus*), correlations between activity, exploration, and risk taking suggest that relative levels of boldness may have ecological and evolutionary significance (Wilson and Godin 2009). Individuals exhibiting higher levels of boldness might also be more susceptible to capture, and selective catch-and-release mortality may cause changes in certain phenotypic frequencies within fish populations (Wilson et al. 2015). Importantly, vulnerability to angling, potentially indicative of relative boldness levels (Uusi-Heikkilä et al. 2008), increased over several generations in replicate experimental populations of largemouth bass (*Micropterus salmoides*), suggesting that angling vulnerability is a heritable trait (Philipp et al. 2009). Increased vulnerability to capture is linked to faster growth rates and greater levels of parental care, so selectively harvesting these putatively bolder fish may reduce both mean adult body size and reproductive output (Cooke et al. 2007; Uusi-Heikkilä et al. 2008; Sutter et al. 2012; Philipp et al. 2015) while also reducing the levels of boldness-linked parental care behaviours in the remaining population (Twardek et al. 2017).

Largemouth bass are the most popular sportfish in North America (Quinn and Paukert 2009). Although there are a variety of harvest regulations used to manage bass populations (Noble 2002) including seasonal closures, length/slot limits, and bag limits, some areas within waterbodies have also been designated as aquatic protected areas (APAs) where angling is prohibited year-round. From a conservation perspective, APAs are effective for increasing density, biomass, size of individuals, and diversity of fish (Halpern 2003) and are commonly used in freshwater systems (e.g., Agardy 1994; Hyrenbach et al. 2000; Saunders et al. 2002; Suski and Cooke 2007). Long-standing APAs provide opportunities to compare both physical and behavioural characteristics between fishes in fully protected areas versus seasonally protected areas. Not surprisingly given their popularity, largemouth bass have been the subject of a variety of studies evaluating catch-and-release mortality (reviewed in Siepker et al. 2007) as well as describing and quantifying FIE (reviewed in Philipp et al. 2015). In addition to demonstrating heritability of boldness-linked behaviours (Philipp et al. 2009), largemouth bass are an ideal FIE study species based on recent findings that different angling techniques appear to selectively target bass of different boldness levels (Wilson et al. 2015). Similarly, largemouth bass in exploited lakes are less vulnerable to capture and demonstrate lower levels of aggression than bass in unexploited lakes, suggesting that angling pressure may have an evolutionary effect on fish behaviour (Philipp et al. 2015). Despite interpopulation evidence supporting recreational angling and FIE in largemouth bass, no comparisons of their behaviour between protected and exploited areas within a single lake have been published to date.

The objective of this project was to determine if established APAs have an effect on the evolution of boldness in largemouth bass as a result of lower fishing pressure. Based on this objective, we predicted that fish would be bolder on average inside the APAs as opposed to those outside the APAs, as they would have been protected from long-term fishing pressure. Fish were also caught by both active and passive capture techniques (angling and hoop nets, respectively) (Hubert et al. 2012) in both protected and non-protected areas. Thus, we also predicted that fish caught by chance via hoop net (i.e., passive technique) would be less bold than those caught via angling. This study provides further insight into the ecological and evolutionary implications of selective harvesting in recreational fisheries and may provide supplementary evidence for fisheries management plans that promote sustainable and diverse wild fish populations.

Methods

Field collections

Between 18 May and 12 June 2015, we captured 105 adult largemouth bass using two different capture methods in Lake Opinicon, Ontario, Canada (44°33′32″N, 76°19′42″W) from several shallow bays inside and outside two APAs. This is an ideal study system, as largemouth bass are under intense seasonal recreational angling pressure. Lake Opinicon has two long-established (>70 years) year-round APAs located in isolated, well-marked bays at either end of the lake that prohibit all forms of fishing including catch-and-release angling. Lake Opinicon has a total area of 890 ha and its two sanctuaries, Murphy Bay and Darlings Bay, are 14.2 and 83 ha, respectively (Keast 1978). Lake Opinicon also reflects ideal largemouth bass habitat, as it is shallow and contains significant numbers of submerged tree trunks and stumps as a result of construction of the Rideau Canal and a corresponding rise in overall water levels (Karst and Smol 2000). There is also a commercial fishery that uses hoop nets outside the sanctuaries, and although largemouth bass cannot be harvested, bycatch mortality does occur (Colotelo et al. 2013). For this study, the first capture method involved actively angling 52 fish (total length 280–474 mm (mean = 361 mm)) using a "wacky-rigged" plastic worm setup. Another 53 individuals were caught passively using unbaited hoop nets (total length 280–451 mm (mean = 361 mm)). Hoop nets were used as our passive capture technique, as the gear does not move throughout the capture process (Hubert et al. 2012). Fish were caught using both capture methods inside ($N = 52$, total length 280–474 mm (mean = 365 mm)) and outside the APAs ($N = 53$, total length 281–445 mm (mean = 357 mm)) (Table 1).

Upon capture, fish were landed as quickly as possible either using a rubberized net (angled fish) or by hand (hoop net). All fish were measured and placed in plastic coolers filled with lake water (45–95 L). Any fish that were deeply hooked, bleeding, or demonstrating abnormal or impaired behaviours (e.g., disequilibrium) were excluded from the study and released. Fish were captured via both methods concurrently, in similar habitat types, and, when applicable, using the same plastic baits. Upon capture, each fish was marked via clipping the tips off of one or more of the spines on the dorsal fin to indicate their area of capture and allow individual identification. Fish were then transported via boat to holding facilities at the Queen's University Biological Station.

Holding conditions and experimental arena

All fish were kept in large cattle trough holding tanks (maximum four fish per 2 m diameter tank, water depth 50 cm) that were supplied with a constant flow of fresh lake water. Fish were kept in the holding tanks for 24 h prior to behavioural trials, and to limit the influence of any additional variables associated with capture or holding stress, they were not fed before experimental testing.

During each behavioural trial, a focal fish was placed into a large, rectangular (2.6 × 6 m) experimental arena (after Wilson et al. 2015) that was separated from the lake with steel mesh at one end. Black plastic blinds were erected around the arena to maintain visual isolation between the fish and the observers. The arena was divided into six regions (each 1 m wide) by five lines of string to assist in tests for activity level of individuals. At the end of the area opposite the steel mesh, there was an acclimation chamber that was used in refuge emergence tests. The inner box of the acclimation chamber was an opaque box with a small opening at the top for the addition of fish and on one side of the box to allow fish to exit once a behavioural trial began. The outer box was a removable steel mesh box placed around the box until the behavioural trial began to prevent fish exiting prematurely. The steel mesh box allowed removal without disturbing individuals inside the box and was covered in black plastic on one side to cover the opening of the inner box.

Behavioural testing

Approximately 24 h after capture, each focal fish was caught using a rubberized net and transferred from the holding tank via a cooler to the inner box of the acclimation chamber. After a 10 min acclimation period, the steel mesh covering the entrance was raised allowing the fish to swim freely into the open area. Each fish was given 10 min to exit the acclimation chamber. In the event fish did not exit after 10 min, they were given the maximum refuge emergence score of 600 s and the chamber was remotely removed from the arena via a suspended rope. Once the fish exited the chamber, refuge emergence time (seconds), activity (number of line crosses over 10 min), and flight-initiation-distance (FID) (centimetres) in response to an approaching object were recorded (after Wilson et al. 2015). If the fish did not exit the chamber, they were given 1 min after the chamber was removed to acclimate in the arena before measuring behavioural metrics. Activity was measured by counting the number of 1 m sections crossed by the individual fish. Afterwards, FID was measured as the minimum distance of a novel object to initiate a flight response. An orange ball (8 cm diameter) mounted on one end of a 1.5 m wooden rod was used as the novel (visual) stimulus (after Kim et al. 2009). Once stationary, the focal fish was approached by the visual stimulus at a fixed speed and angle, starting at a distance of 1.5 m (Wilson et al. 2015). Following the first trial, fish were placed back in the holding tank and held overnight prior to a second identical behavioural trial the following day.

Data analyses

Two-way analysis of covariance (ANCOVA) tests were run using capture method, location of capture, and the interaction between method and location of capture as predictor variables, fish size as a covariate, and three separate measures of boldness (refuge emergence, activity, and FID) as response variables. We tested each response variable for normality and any variable that did not follow a normal distribution (Shapiro–Wilk test, $P < 0.05$) was ranked to allow testing using analysis of variance (ANOVA) (Scheirer et al. 1976).

Spearman's rank correlation tests were used to compare individual behavioural traits (refuge emergence, activity, and FID) and fish size. To test for the presence of a boldness syndrome, we used principal components analysis (PCA) to collapse the individual behavioural traits into a first principal components score (PC1). Individual PC1 scores for each day were then compared using Spearman's rank correlation test to test whether the suites of behaviours that we measured varied consistently over time and could therefore be described as representative of individual behavioural types. We used factorial two-way ANOVA using capture method and location of capture predictor variables and the PC1 scores as the response variable. Tukey's HSD post hoc test was also conducted on gear type within APAs and outside the APAs. All analyses were conducted using R v3.0.2 (R Core Team 2015) and figures were generated using SigmaPlot v11.0.

Results

We collected 53 bass from the APAs (26 angling and 27 hoop net) and 52 from outside the APAs (26 angling and 26 hoop net). Fish caught by active methods (angling) demonstrated significantly higher levels of activity than fish caught by passive methods (hoop nets) ($F_{[1,100]} = 6.2105$, $P = 0.014$) (Fig. 1*b*; Table 2). As well, a significant relationship was observed between fish length and activity level, with larger fish demonstrating more activity than smaller fish ($F_{[1,100]} = 4.7088$, $P = 0.032$) (Table 2). Boldness did not differ significantly with capture method, but a trend was detected towards angling selecting for bolder fish ($F_{[3,98]} = 2.3790$, $P = 0.0744$) (Figs. 1*a* and 1*b*; Table 2). Location (APA or non-APA) also did not significantly influence behavioural metrics; however, there was a trend towards fish from outside the APAs being more active than fish caught inside the APAs ($F_{[1,100]} = 3.2374$, $P = 0.075$) (Fig. 1*b*; Table 2). There was a significant difference between activity levels of fish caught by different capture techniques inside the APAs, with angled fish demonstrating significantly higher activity levels than fish caught by hoop net ($P < 0.05$) (Fig. 1*b*). There were no significant differences in refuge emergence time, FID, size, or PC1 scores between fish caught by the different methods or from the different locations (all $P > 0.05$) (Table 2).

Spearman's rank correlation tests revealed that all individual behavioural traits were significantly positively correlated between trials (all $P < 0.01$). As well, refuge emergence was negatively correlated with activity level ($P < 0.01$). PC1 (boldness) scores showed significant correlations between trials on successive days, indicating the presence of a behavioural syndrome in individual bass (Table 3). In general, individuals that emerged faster from the refuge were more exploratory and had shorter FIDs than fish that took longer to emerge (Table 4).

Discussion

As predicted, the active targeting (i.e., capture via angling) of largemouth bass does appear to target more mobile individuals when compared to more passive capture techniques such as hoop nets. Interestingly, we did not observe this same relationship when considering refuge emergence time and FID separately, nor did we observe any significant differences in behaviour between fish captured inside and outside the APAs in any of our behavioural metrics. That being said, both activity and refuge emergence time were strongly correlated across experimental days as well as together, with more active individuals having shorter time to emergence from the refuge. We also observed significant positive correlations across experimental days in our composite PC1 scores incorporating all behavioural traits, perhaps suggesting

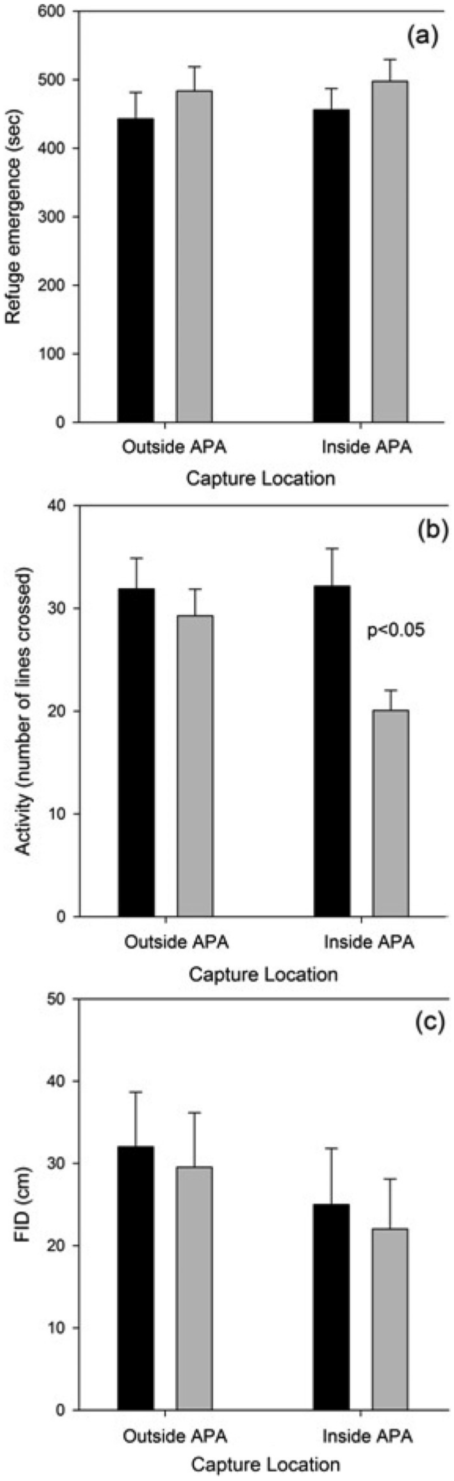

Fig. 1. Mean (±SE) observed behaviours demonstrated by largemouth bass (*Micropterus salmoides*) caught inside and outside APAs by angling (black) and hoop net (grey). (*a*) Refuge emergence time, (*b*) activity levels (number of lines crossed during 10 min observations), and (*c*) flight-initiation-distance. The *P* values were obtained from Tukey's HSD post hoc test.

the presence of a behavioural syndrome (Sih et al. 2004; Archard and Braithwaite 2011) with ecological significance and of particular relevance in a FIE context.

Our results suggest that APAs may mitigate the effects of FIE on exploited bass populations by preserving a wider variety of activity levels in protected areas. These results might be indicative of fisheries-induced selection acting to reduce variation in behavioural traits without exerting directional selection towards new mean trait values. In association with reduced selection on activity-linked behaviours, bass inside APAs might experience increased intraspecific competition due to reduced angling pressure. Moreover, APAs could act as refugia for bass seeking structured habitat with sufficient cover, thus enabling increases in population density (Savino and Stein 1989; Bilhete and Grant 2016). Intraspecific competition has been known to enhance behavioural flexibility, particularly with foraging specialization and diet requirements (reviewed in Jones and Post 2016), which may have occurred inside the APAs. Despite optimality-based assumptions, homogeneity of individuals with high activity levels may not be beneficial at the population level. For example, more active, potentially risk-prone individuals may have higher metabolism (Sutter et al. 2012) and expend more energy foraging, potentially decreasing investments in reproduction and nesting (Folkvord et al. 2014). Retention of low-activity phenotypes may be beneficial for behaviours such as nest attentiveness, reducing tradeoffs between high activity and nest guarding (Steinhart et al. 2005; Härkönen et al. 2014).

Although home ranges of largemouth bass have been reported to be small (e.g., Winter 1977; Mesing and Wicker 1986), there is limited information on the movement of largemouth bass within Lake Opinicon and surrounding waterbodies. Despite demonstrating high nest fidelity (e.g., Waters and Noble 2004), it is possible that post-nesting bass situated close to APA boundaries may frequently migrate outside the protected area and vice versa. However, fish that cross APA boundaries are still likely receiving more protection than fish that are situated farther away from the APAs (Demille 2010). As largemouth bass have high nest site fidelity and limited migration when spawning, APAs may have the largest and most observable impact on bass behaviour during the nesting season, thus positively influencing egg survival. Although angling bass is prohibited throughout the spawning period in the region where the research took place, largemouth bass may still be unintentionally caught and temporarily removed from the nest outside the APAs, exposing their eggs to higher levels of predation (Suski et al. 2003). Furthermore, nest protection inside APAs in tandem with the heritability of bold phenotypes (sensu Philipp et al. 2009) may allow APAs to act as a source population of bolder individuals for the population outside the APAs. That being said, the two APAs within Lake Opinicon only consist of 12.3% of the total surface area, which may or may not be sufficient protection to preserve behavioural phenotype diversity over longer time scales. Additional comparative analyses with other populations as well as genetic analysis of subpopulations would provide important insights regarding the movement of offspring and potential source/sink dynamics.

FIE, resulting from the selection of various traits over time, can alter the abundance of phenotypes within a population, which may have ecological consequences. Our findings suggest that protected areas may promote the diversification of behavioural traits, notably related to activity; however, with regard to our geographic scope and chosen behavioural traits, we cannot provide direct evidence that the APAs in Lake Opinicon are effective in maintaining boldness-related behaviours in largemouth bass. In contrast, we provide evidence that angling does in fact target bolder individuals, suggesting that APAs should have the potential to prevent selection against some traits such as high activity levels. These results on the relationship between gear type and activity level in largemouth bass, and within-context behavioural correlations, provide valuable information to further investigate the potential for FIE within recreational fisheries. It remains unclear the extent to which APAs that exclude fishing year-round versus only during the spawning period for bass (see Suski et al. 2002) may achieve conservation targets. Similarly, it is unclear the

Table 2. MANCOVA results of behavioural responses demonstrated by largemouth bass (*Micropterus salmoides*) caught via hoop net or angling inside and outside APAs.

	Factor (multivariate response)	*F*	df	*P*
	Method	2.3790	3, 98	0.07436*
	Location	1.6194		0.18979
	Method × location	1.0985		0.35359
	Size	1.9861		0.12106
Behavioral metric	Factor (univariate response)			
Refuge emergence	Method	1.9669	1, 100	0.1639
	Location	0.0010		0.9750
	Method × location	0.0772		0.7817
	Size	0.4216		0.5176
Activity	Method	6.2105		**0.01434**
	Location	3.2374		0.07499*
	Method × location	2.5322		0.11470
	Size	4.7088		**0.03238**
FID	Method	0.3521		0.5543
	Location	1.6869		0.1970
	Method × location	0.6989		0.2443
	Size	1.3717		0.4052
PC1 score	Method	2.2302		0.1385
	Location	0.6858		0.4096
	Method × location	0.0216		0.8836
	Size	1.0729		0.3028

Note: Bold font signifies statistical significance ($P < 0.05$) and asterisks indicate near-significance ($0.1 > P > 0.05$).

Table 3. Spearman's rank correlation test coefficients between behavioural responses demonstrated by largemouth bass (*Micropterus salmoides*) on subsequent observation days.

Variable 1	Variable 2	r_s	*P*
Refuge emergence (s)	Size (mm)	−0.065	0.5086
Refuge emergence (s)	FID (cm)	0.142	0.1487
Activity (no. of line crosses)	Size (mm)	0.179	0.06837*
Activity (no. of line crosses)	FID (cm)	0.059	0.5492
FID (cm)	Size (mm)	0.086	0.3826
Refuge emergence (s)	Activity (no. of line crosses)	−0.292	**0.002504**
Refuge emergence (s) (Day 1)	Refuge emergence (s) (Day 2)	0.458	**<0.0001**
Activity (no. of line crosses) (Day 1)	Activity (no. of line crosses) (Day 2)	0.289	**0.002783**
FID (cm) (Day 1)	FID (cm) (Day 2)	0.539	**<0.0001**
PC1 (Day 1)	PC1 (Day 2)	0.457	**<0.0001**

Note: Bold font signifies statistical significance ($P < 0.05$) and asterisks indicate near-significance ($0.1 > P > 0.05$).

Table 4. PCA loadings of within-context behavioural variables used to generate a PC score (PC1) for boldness in largemouth bass (*Micropterus salmoides*).

Behavioural context	Behaviours within context	Loadings for PC1	Variation explained
Boldness	Refuge emergence	−0.9991	95.97%
	General activity	0.0195	
	FID	−0.0364	

extent to which APAs that allow catch-and-release (i.e., no-take APAs) but prohibit harvest would protect fish phenotypic diversity (Cooke et al. 2006). With greater focus on ecosystem approaches to fisheries management and maintenance of phenotypic diversity reflecting the potential for FIE (see Ward et al. 2016), APAs will presumably become even more common as a form of evolutionarily enlightened management (Ashley et al. 2003).

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References

Agardy, M.T. 1994. Advances in marine conservation: the role of marine protected areas. Trends Ecol. Evol. **9**(7): 267–270. doi:10.1016/0169-5347(94)90297-6. PMID:21236850.

Allendorf, F.W., and Hard, J.J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc. Natl. Acad. Sci. U.S.A. **106**(S1): 9987–9994. doi:10.1073/pnas.0901069106. PMID:19528656.

Alós, J., Palmer, M., Catalan, I.A., Alonso-Fernández, A., Basterretxea, G., Jordi, A., Buttay, L., Morales-Nin, B., and Arlinghaus, R. 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Mar. Ecol. Progr. Ser. **503**: 219–233. doi:10.3354/meps10745.

Archard, G.A., and Braithwaite, V.A. 2011. Increased exposure to predators increases both exploration and activity level in *Brachyrhaphis episcopi*. J. Fish Biol. **78**(2): 593–601. doi:10.1111/j.1095-8649.2010.02880.x. PMID:21284637.

Arlinghaus, R., and Cooke, S.J. 2009. Recreational fisheries: socioeconomic importance, conservation issues and management challenges. *In* Recreational hunting, conservation and rural livelihoods: science and practice. *Edited by* B. Dickson, J. Hutton, and W.M. Adams. Blackwell Publishing Ltd. doi:10.1002/9781444303179.

Ashley, M.V., Willson, M.F., Pergams, O.R.W., O'Dowd, D.J., Gende, S.M., and Brown, J.S. 2003. Evolutionarily enlightened management. Biol. Conserv. **111**(2): 115–123. doi:10.1016/S0006-3207(02)00279-3.

Bilhete, C., and Grant, J.W.A. 2016. Short-term costs and benefits of habitat complexity for a territorial fish. Ethology, **122**(2): 151–157. doi:10.1111/eth.12456.

Biro, P.A., and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Natl. Acad. Sci. U.S.A. **105**(8): 2919–2922. doi:10.1073/pnas.0708159105. PMID:18299567.

Brownscombe, J.W., Bower, S.D., Bowden, W., Nowell, L., Midwood, J.D., Johnson, N., and Cooke, S.J. 2014. Canadian recreational fisheries: 35 years of social, biological, and economic dynamics from a national survey. Fisheries, **39**(6): 251–260. doi:10.1080/03632415.2014.915811.

Colotelo, A.H., Cooke, S.J., Blouin-Demers, G., Murchie, K.J., Haxton, T., and Smokorowski, K.E. 2013. Influence of water temperature and net tending frequency on the condition of fish bycatch in a small-scale inland commercial fyke net fishery. J. Nat. Conserv. **21**(4): 217–224. doi:10.1016/j.jnc.2013.01.001.

Cooke, S.J., Schreer, J., Wahl, D., and Philipp, D. 2002*a*. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Am. Fish. Soc. Symp. **31**: 489–512.

Cooke, S.J., Schreer, J.F., Dunmall, K.M., and Philipp, D.P. 2002*b*. Strategies for quantifying sublethal effects of marine catch-and-release angling: insights from novel freshwater applications. Am. Fish. Soc. Symp. **30**: 121–134.

Cooke, S.J., Danylchuk, A.J., Danylchuk, S.E., Suski, C.D., and Goldberg, T.L. 2006. Is catch-and-release recreational angling compatible with no-take marine protected areas? Ocean Coast. Manage. **49**(5–6): 342–354. doi:10.1016/j.ocecoaman.2006.03.003.

Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H., and Philipp, D.P. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiol. Biochem. Zool. **80**(5): 480–490. doi:10.1086/520618. PMID:17717811.

Demille, M.J. 2010. The behaviour of Largemouth Bass in Lake Opinicon, Ontario: a biological perspective for the evaluation of murphy bay fish sanctuary. M.Sc. thesis, Department of Biology, Queen's University, Kingston, Ont.

Dunmall, K.M., Cooke, S.J., Schreer, J.F., and Mckinley, R.S. 2001. The effect of scented lures on the hooking injury and mortality of smallmouth bass caught by novice and experienced anglers. N. Am. J. Fish. Manage. **21**(1): 242–248. doi:10.1577/1548-8675(2001)021<0242:TEOSLO>2.0.CO;2.

Elvidge, C.K., Chuard, P.J.C., and Brown, G.E. 2016. Local predation risk shapes spatial and foraging neophobia patterns in Trinidadian guppies. Curr. Zool. **62**(5): 457–462. doi:10.1093/cz/zow013.

Folkvord, A., Jørgensen, C., Korsbrekke, K., Nash, R.D.M., Nilsen, T., and Skjæraasen, J.E. 2014. Trade-offs between growth and reproduction in wild Atlantic cod. Can. J. Fish. Aquat. Sci. **71**(7): 1106–1112. doi:10.1139/cjfas-2013-0600.

Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl. **13**(1): S117–S137. doi:10.1890/1051-0761.

Härkönen, L., Hyvärinen, P., Paappanen, J., and Vainikka, A. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **71**(12): 1900–1909. doi:10.1139/cjfas-2014-0221.

Heino, M., and Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bull. Mar. Sci. **70**(2): 639–656.

Hubert, W.A., Pope, K.L., and Dettmers, J.M. 2012. Passive capture techniques. *In* Fisheries techniques. 3rd ed. American Fisgeries Society, Bethesda, Md. pp. 223–265.

Hyrenbach, K.D., Forney, K.A., and Dayton, P.K. 2000. Marine protected areas and ocean basin management. Aquat. Conserv. Mar. Freshw. Ecosyst. **10**: 437–458. doi:10.1002/1099-0755(200011/12)10:6<437::aid-aqc425>3.0.co;2-q.

Jennings, S., Greenstreet, S.P.R., and Reynolds, J.D. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. J. Anim. Ecol. **68**(3): 617–627. doi:10.1046/j.1365-2656.1999.00312.x.

Jones, A.W., and Post, D.M. 2016. Does intraspecific competition promote variation? A test via synthesis. Ecol. Evol. **6**: 1646–1655. doi:10.1002/ece3.1991. PMID:27087931.

Karst, T.L., and Smol, J.P. 2000. Paleolimnological evidence of limnetic nutrient concentration equilibrium in a shallow, macrophyte-dominated lake. Aquat. Sci. **62**(1): 20–38. doi:10.1007/s000270050073.

Keast, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fishes, **3**(1): 7–31. doi:10.1007/BF00006306.

Kim, J.W., Brown, G.E., Dolinsek, I.J., Brodeur, N.N., Leduc, A.O.H.C., and Grant, J.W.A. 2009. Combined effects of chemical and visual information in eliciting antipredator behaviour in juvenile Atlantic salmon *Salmo salar*. J. Fish Biol. **74**(6): 1280–1290. doi:10.1111/j.1095-8649.2009.02199.x. PMID:20735631.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Mar. Ecol. Progr. Ser. **335**: 271–277. doi:10.3354/meps335271.

Mesing, C.L., and Wicker, A.M. 1986. Home range, spawning migrations, and homing of radio-tagged Florida Largemouth Bass in two central Florida lakes. Trans. Am. Fish. Soc. **115**(2): 286–295. doi:10.1577/1548-8659(1986)115<286:HRSMAH>2.0.CO;2.

Muoneke, M.I., and Childress, W.M. 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. **2**(2): 123–156. doi:10.1080/10641269409388555.

Noble, R.L. 2002. Reflections on 25 years of progress in black bass management. Am. Fish. Soc. Symp. **31**: 419–431.

Philipp, D.P., Cooke, S.J., Claussen, J.E., Koppelman, J.B., Suski, C.D., and Burkett, D.P. 2009. Selection for vulnerability to angling in largemouth bass. Trans. Am. Fish. Soc. **138**(1): 189–199. doi:10.1577/T06-243.1.

Philipp, D.P., Claussen, J.E., Koppelman, J.B., Stein, J.A., Cooke, S.J., Suski, C.D., Wahl, D.H., Sutter, D.A.H., and Arlinghaus, R. 2015. Fisheries-induced evolution in largemouth bass: linking vulnerability to angling, parental care, and fitness. Am. Fish. Soc. Symp. **82**: 223–234.

Quinn, S., and Paukert, C. 2009. Centrarchid fisheries. *In* Centrarchid fishes: diversity, biology and conservation. Wiley. pp. 312–330.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. **82**(2): 291–318. doi:10.1111/j.1469-185X.2007.00010.x. PMID:17437562.

Saunders, D.L., Meeuwig, J.J., and Vincent, A.C.J. 2002. Freshwater protected areas: strategies for conservation. Conserv. Biol. **16**(1): 30–41. doi:10.1046/j.1523-1739.2002.99562.x.

Saura, M., Morán, P., Brotherstone, S., Caballero, A., Álvarez, J., and Villanueva, B. 2010. Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). Freshw. Biol. **55**(4): 923–930. doi:10.1111/j.1365-2427.2009.02346.x.

Savino, J.F., and Stein, R.A. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environ. Biol. Fishes, **24**(4): 287–293. doi:10.1007/BF00001402.

Scheirer, C.J., Ray, W.S., and Hare, N. 1976. The analysis of ranked data derived from completely randomized factorial designs. Biometrics, **32**(2): 429–434. doi:10.2307/2529511. PMID:953139.

Siepker, M.J., Ostrand, K.G., Cooke, S.J., Philipp, D.P., and Wahl, D.H. 2007. A review of the effects of catch-and-release angling on black bass, *Micropterus* spp.: implications for conservation and management of populations. Fish. Manag. Ecol. **14**(2): 91–101. doi:10.1111/j.1365-2400.2007.00529.x.

Sih, A., Bell, A., and Johnson, J.C. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. **19**(7): 372–378. doi:10.1016/j.tree.2004.04.009. PMID:16701288.

Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Can. J. Fish. Aquat. Sci. **59**(2): 361–371. doi:10.1139/f02-015.

Steinhart, G.B., Sandrene, M.E., Weaver, S., Stein, R.A., and Marschall, E.A. 2005. Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators. Behav. Ecol. **16**(2): 427–434. doi:10.1093/beheco/ari006.

Suski, C.D., and Cooke, S.J. 2007. Conservation of aquatic resources through the use of freshwater protected areas: opportunities and challenges. Biodivers. Conserv. **16**(7): 2015–2029. doi:10.1007/s10531-006-9060-7.

Suski, C.D., Kubacki, M.R., Phelan, F.J.S., and Philipp, D.P. 2002. The use of community-based sanctuaries for protecting smallmouth bass and largemouth bass from angling. *In* Black bass: ecology, conservation, and management. *Edited by* D.P. Philipp and M.S. Ridgway. American Fisheries Society, Bethesda, Md. pp. 371–378.

Suski, C.D., Svec, J.H., Ludden, J.B., Phelan, F.J.S., and Philipp, D.P. 2003. The effect of catch-and-release angling on the parental care behavior of male smallmouth bass. Trans. Am. Fish. Soc. **132**: 210–218. doi:10.1577/1548-8659(2003)132<0210:TEOCAR>2.0.CO;2.

Sutter, D.A.H., Suski, C.D., Philipp, D.P., Klefoth, T., Wahl, D.H., Kersten, P., Cooke, S.J., and Arlinghaus, R. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proc. Natl. Acad. Sci. U.S.A. **109**(51): 20960–20965. doi:10.1073/pnas.1212536109. PMID:23213220.

Twardek, W.M., Elvidge, C.K., Wilson, A.D.M., Algera, D.A., Zolderdo, A.J., Lougheed, S.C., and Cooke, S.J. 2017. Do protected areas mitigate the effects of fisheries-induced evolution on parental care behaviour of a teleost fish? Aquat. Conserv. Mar. Freshw. Ecosyst.: 1–8. doi:10.1002/aqc.2718.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T., and Arlinghaus, R. 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol. Evol. **23**(8): 419–421. doi:10.1016/j.tree.2008.04.006. PMID:18582988.

Ward, T.D., Algera, D.A., Gallagher, A.J., Hawkins, E., Horodysky, A., Jørgensen, C., Killen, S.S., McKenzie, D.J., Metcalfe, J.D., Peck, M.A., Vu, M., and Cooke, S.J. 2016. Understanding the individual to implement the ecosystem approach to fisheries management. Conserv. Physiol. **4**(1): cow005. doi:10.1093/conphys/cow005. PMID:. PMID:27293757.

Waters, D.S., and Noble, R.L. 2004. Spawning season and nest fidelity of largemouth bass in a tropical reservoir. N. Am. J. Fish. Manage. **24**(4): 1240–1251. doi:10.1577/M03-048.1.

Wilson, A.D.M., and Godin, J.-G.J. 2009. Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. Behav. Ecol. **20**(2): 231–237. doi:10.1093/beheco/arp018.

Wilson, A.D.M., Binder, T.R., McGrath, K.P., Cooke, S.J., and Godin, J.-G.J. 2011. Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. Can. J. Fish. Aquat. Sci. **68**(5): 749–757. doi:10.1139/f2011-019.

Wilson, A.D.M., Brownscombe, J.W., Sullivan, B., Jain-Schlaepfer, S., and Cooke, S.J. 2015. Does angling technique selectively target fishes based on their behavioural type? Plos ONE, **10**(8): e0135848. doi:10.1371/journal.pone.0135848. PMID:26284779.

Wilson, D.S., Coleman, K., Clark, A., and Biederman, L. 1993. Shy bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. J. Comp. Psychol. **107**(3): 250–260. doi:10.1037/0735-7036.107.3.250.

Wilson, D.S., Clark, A.B., Coleman, K., and Dearstyne, T. 1994. Shyness and boldness in humans and other animals. Trends Ecol. Evol. **9**(11): 442–446. doi:10.1016/0169-5347(94)90134-1. PMID:21236920.

Winter, J.D. 1977. Summer home range movements and habitat use by four largemouth bass in Mary Lake, Minnesota. Trans. Am. Fish. Soc. **106**(4): 323–330. doi:10.1577/1548-8659(1977)106<323:SHRMAH>2.0.CO;2.