



ARTICLE

# Comparative Behavior of Wild Bluegill Captured Inside and Outside of a Long-Standing Aquatic Protected Area

Emily N. Moynes

*Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada*

Michael J. Lawrence\* 

*Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada*

Aaron J. Zolderdo , Tanya S. Prystay, Alice E.I. Abrams, Peter Holder, and Steven J. Cooke 

*Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada*

---

## Abstract

In recreational fisheries it is understood that individual fish that exhibit bolder personality traits have a tendency to be removed from the population (i.e., fishing mortality via harvest or catch-and-release mortality), while more timid individuals remain. The use of aquatic protected areas (APAs) has been promoted as a means of offsetting the negative consequences that are associated with fishing mortality by protecting the full suite of phenotypes. However, little work has investigated whether APAs are able to maintain heterogeneity in behavioral traits in wild fish. We attempted to address this question by using wild Bluegill *Lepomis macrochirus* from Lake Opinicon, a freshwater system consisting of both an APA and heavily fished areas. The Bluegill were obtained via angling from three zones in the lake: the main lake area (i.e., fished), the APA (which has been in place since the 1940s), and a transitional zone between these two areas. In the laboratory, the Bluegill were subjected to two behavioral assessments, a Z-maze and a flight-initiation-distance (FID) test, to address differences in boldness and risk-taking between these populations. No significant effects of capture zone were detected for any of the behavioral metrics that were assessed in the maze trial. However, individuals that originated from the main lake population had significantly higher FID scores than the fish from the transitional zone and the APA did, indicating that they were more timid. Our results suggest that fisheries activities may only be acting only on specific traits, which may explain some of the null results that are presented here. Nevertheless, our study provides evidence that APAs are providing a reservoir of less timid individuals, which is consistent with an evolutionarily enlightened management strategy.

---

Fishing mortality occurs in both freshwater and marine systems as a result of harvest or incidental mortality (Botsford et al. 1997; Cooke and Cowx 2004; Allan et al. 2005). Both active and passive fisheries gears including hook-and-line angling techniques, baited traps, and/or targeted netting regimes can impose selection pressures on a

targeted fish stock. Selection in this context arises through the selective removal of individuals that exhibit specific phenotypes (e.g., boldness; Diaz Puali and Sih 2017), which render them more vulnerable to capture and harvest. This type of selection pressure can have population-level effects including reduced age and size at maturity

---

\*Corresponding author: m\_lawrence27@live.ca  
Received August 22, 2019; accepted November 20, 2019

and reduced reproductive investment, a phenomenon referred to as fisheries-induced evolution (FIE; Heino and Godø 2002). Fisheries-induced evolution requires that the trait of interest is heritable and is subject to artificial selection by fisheries activities (Uusi-Heikkilä et al. 2008; Heino et al. 2015; Hollins et al. 2018). For example, the extensive harvest of Atlantic Cod *Gadus morhua* in maritime Canada resulted in a declining average body mass as well as earlier maturation time over the ~20-year monitoring period, suggesting FIE (Olsen et al. 2004; Kuparinen and Merilä 2007). Because of the role that fisheries activities may play in potentially modifying the population structure of species that are of significant economic value and its implications for effective fisheries management, it has become an increasingly relevant field of study in recent years (Hutchings 2009; Heino et al. 2013; Hollins et al. 2018).

Intraspecific variation in fish personality and behavioral phenotypes are thought to be subject to fisheries-based selection. Here, fish behavior is often framed within the bold–shy continuum, wherein bolder individuals exhibit riskier behavioral phenotypes, lack neophobia, and react proactively to environmental stimuli (Wilson et al. 1993, 1994; Réale et al. 2007; Thomson et al. 2011). Furthermore, these traits appear to have an underlying genetic basis in teleosts (Oswald et al. 2012, 2013) and are believed to be associated with specific fitness benefits within certain environmental conditions (Smith and Blumstein 2008; Sih et al. 2012). Consequently, intraspecific variation in fish behavioral phenotypes and personality is likely to be subject to both selective mortality by fisheries activities and by FIE at large (Conrad et al. 2011; Philipp et al. 2015). While information on fisheries–fish behavior interactions as well as in the ecological consequences of fisheries activities is rather scant in the literature (Ioannou et al. 2008; Uusi-Heikkilä et al. 2008; Heino et al. 2015), several studies have indicated the presence of population-level behavioral changes that are associated with fisheries activities. In centrarchids, it has been documented that individuals that exhibit “bold” behavioral phenotypes are more vulnerable to angling events (Suski and Philipp 2004; Philipp et al. 2015; Twardek et al. 2017) and this can have population-level consequences, with respect to shifts in behavioral phenotypes, in heavily exploited populations (reviewed in Philipp et al. 2015; Twardek et al. 2017). These shifts generally include a reduction in the aggression levels that are exhibited by nesting adult black bass. Similar observations have been made in other species of teleosts as well (Biro and Post 2008; Alós et al. 2014, 2015; Härkönen et al. 2014). Indeed, in captive Rainbow Trout *Oncorhynchus mykiss* that were fished extensively over a 5-d period in controlled lakes, a significantly higher proportion of “bold” genotype trout were removed from the system, relative to “shy” genotyped fish (Biro and Post

2008). Together, these results suggest that fisheries activities can remove bolder individuals from the population, resulting in a more homogenous behavioral phenotype structure. However, this may not always be the case because capture vulnerability is not necessarily a product of individual behavioral characteristics (Vainikka et al. 2016). Further work is needed to address some of the proximate mechanisms that underlie how fisheries activities influence population structure.

From a management perspective, the effects of fishing mortality may be offset by the use of aquatic protected areas (APAs; Ashley et al. 2003; Westera et al. 2003; Watson et al. 2007), areas of an aquatic system where fishing (or harvest) is prohibited for all or part of the year (Suski and Cooke 2007; Harrison et al. 2016). As FIE requires an extraction of fish from the local population, APAs have been proposed as a means of conserving genetic/phenotypic diversity within a target population and offsetting the deleterious effects that are associated with fisheries activities (Lauck et al. 1998; Ashley et al. 2003; Baskett et al. 2005; Conrad et al. 2011). However, investigations into how APAs conserve behavioral phenotypic diversity remain relatively unknown. Thus, the purpose of this work was to address how APAs can (1) influence the population structure of teleost fish from a behavioral phenotypic perspective and (2) serve as an evolutionarily informed tool for effective fisheries management.

We tested the hypothesis that fish that were captured from regions of high fishing pressure (i.e., bold fish) would exhibit more timid behavioral phenotypes than those that were taken from protected regions (i.e., fish from the APAs) due to the removal of more vulnerable individuals in the heavily fished regions. To do so, we used the Bluegill *Lepomis macrochirus* as a model because of its importance in freshwater commercial and recreational fisheries. We took advantage of long-standing APAs that were initiated in the 1940s in Lake Opinicon in eastern Ontario. Fish that were captured from the field were subjected to behavioral assessments by using a Z-maze trial to assess their boldness and exploratory behaviors coupled with a flight-initiation test to quantify individual risk perception.

## METHODS

*Study site and historical context.*—Lake Opinicon (Chaffey's Lock, Ontario, Canada; 44°33'32"N, 76°19'42"W) is situated within the Rideau Lakes watershed and forms a stretch of the Rideau Canal Navigational Channel, which bisects through southeastern Ontario, Canada. The watershed at large is a popular destination for recreational angling (Ontario Ministry of Natural Resources and Forestry 2015) and has numerous commercial fisheries throughout the

region as well (Burns 2007). On lake Opinicon specifically, centrarchid panfish species (Rock Bass *Ambloplites rupestris*, Bluegill, and Pumpkinseed *Lepomis gibbosus*) make up approximately 27% of the recreational angler's catch (Ontario Ministry of Natural Resources 1995) and at the time of this writing there remains a single commercial fisheries operator on the lake (A.J.Z., personal observation). Throughout the earlier part of the century, there were concerns that Largemouth Bass *Micropterus salmoides* were being overharvested throughout the Rideau Lakes system, prompting fisheries managers to establish year-round, no-take fish sanctuaries (Ontario Department of Game and Fisheries 1946), which had the spin-off effect of creating an APA for the multitude of other species that inhabited the area. Currently, Lake Opinicon has two main APAs, Murphys Bay and Darlings Bay, and under Ontario Ministry of Natural Resources and Forestry Law they are completely off-limits to recreational and commercial fisheries year-round. All of the other areas of the lake are subject to fisheries activities (reviewed in Zolderdo et al. 2019). Like most of the lake, these APAs are quite shallow (>6 m deep) and consist of large swaths of submergent vegetation and sunken woody debris, providing optimal habitat for centrarchid fishes, notably Largemouth Bass and the two resident sunfish species, Pumpkinseed and Bluegill.

*Field collections and holding conditions.*—Bluegill ( $n = 107$ ; mass =  $33.7 \pm 6.8$  g [mean  $\pm$  SD]; total length (TL) =  $12.8 \pm 0.7$  cm) were collected from Lake Opinicon from July 10 to 26, 2017. The fish were angled using standardized tackle consisting of size 2 circle hooks that were baited with small pieces of live earthworm *Lumbricus* sp. Fishing was conducted in similar habitat types in three distinct regions of the lake: an off-limits APA with no fishing pressure (Darlings Bay,  $44^{\circ}31'56''\text{N}$ ,  $76^{\circ}22'2.7''\text{W}$ ; TL =  $12.9 \pm 0.7$  cm;  $n = 37$ ), a transition zone that is adjacent to the APA (0–1 km outside of the APA; TL =  $12.8 \pm 0.7$  cm;  $n = 35$ ), and the main lake, which is under fishing pressure from both commercial and recreational fishing (>3 km outside of the APA; TL =  $12.8 \pm 0.7$  cm;  $n = 35$ ). While information is limited, prior works have found that gradients in fishing pressures generally correspond with a gradient in the behavioral phenotype of the fish, with fish becoming, on average, bolder as one approaches no-take APAs (e.g., Alós et al. 2015; Bergseth et al. 2016). Consequently, we were interested in attempting to quantify whether there was such a behavioral gradient and to our knowledge no such works have addressed this effect in freshwater APAs. We were also confident that, given the small home range ( $0.0072$  km<sup>2</sup> in lotic systems and upwards of 500 m in lentic systems) and high site fidelity in Bluegill (reviewed in Warren 2009), the distances that we used to delineate the main lake (>3 km from the APA) and the transitional regions (0–1 km outside of the APA) should reasonably represent the fish that

are resident to these regions (i.e., fish were not moving between lake regions). Fishing was standardized across similar habitat types to avoid the potential biases that are associated with ecomorphs or habitat-specific differences in the individual's behavioral phenotype (Kobler et al. 2011; Wolf and Weissing 2012). We also acknowledge that perceived predation risk may have biased our sampling towards selecting bolder individuals (i.e., shy fish likely avoided exposure in the open areas where fishing occurred), but as is detailed in the discussion this was unlikely because predation risk is relatively low for such large Bluegill in this system (e.g., Werner et al. 1983; Shoup et al. 2003).

All of the fish were measured on the boat at the time of capture and subsequently placed in a 155-L plastic cooler. Any fish with a parasite load that was greater than 2 (ranked 0–5; 0 = none, 5 = high density) or that was injured in any way was immediately released back into the lake, as parasite load has been found to affect fish behavior (Barber et al. 2000). To indicate the zone in which each fish was caught, a small clip to the caudal fin was made upon capture. The Bluegill were then promptly transported to Queen's University Biological Station (Chaffey's Lock, Ontario, Canada) and held for 24–48 h in outdoor tanks with a continuous inflow of lake water (~300 L; O<sub>2</sub> > 90% saturation; water temperatures of 24–26°C) and a seasonally appropriate illumination cycle (15 h light : 9 h dark). The fish were not fed during any of their time in captivity in order to standardize hunger status. All of the experimental procedures were conducted with the approval of the Carleton University Animal Care Committee (Animal Use Protocol 104281) according to the guidelines that have been established by the Canadian Council on Animal Care.

### Behavioral Testing

*Z-maze behavioral trials.*—The Z-maze trial that we used was similar to that described in Chapman et al. (2010). The Z-maze (Figure 1; 103.3 cm in length  $\times$  80.4 cm in width) consisted of a blackened, gated refuge box (40.5  $\times$  19.8 cm) in a corner that emerged to an open environment that was separated by three black partitions to form a “Z” pattern. The arena was lit by diffuse overhead fluorescent lighting. The open environment contained a grid of 18 squares (20  $\times$  20 cm) that were used to track the movement of the fish through the maze. The water depth was maintained at 18.0 cm.

At the onset of each trial, the maze was filled with fresh lake water ( $23.6^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$  [mean  $\pm$  SD]; O<sub>2</sub> >90% saturation) and a focal fish was obtained from the holding tank. The fish were moved in a small water-filled bucket to minimize the duration of their exposure to air. The test fish were then quickly transferred to the refuge compartment and allowed 2 min to acclimate before the

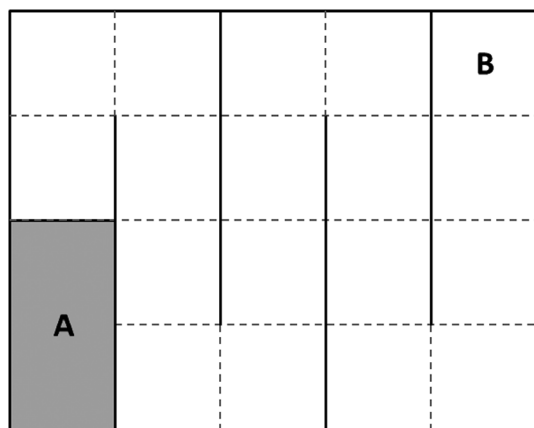


FIGURE 1. The “Z” maze tank. The (A) refuge box is in gray, and (B) indicates the end of the maze. The thickened black lines represent the partitions, and the dashed gray lines represent the 18 squares that are noted as lines that were crossed by the focal fish.

gate was opened. The treatment groups were assayed in the maze in the following systematic randomized order: APA, transition zone, and then main lake fish. On any given day, a maximum of 14 focal fish were run through the maze, with the trial consisting of a balanced experimental design (i.e., ~4 fish from each population). At the onset of opening the refuge gate, the fish was given 10 min to emerge from the refuge. Refuge emergence was defined as the time when more than half of the fish's body was outside of the refuge compartment. If the fish emerged within the 10 min, the emergence time was recorded and the fish was given an additional 10 min to explore the maze. If the fish did not emerge within the 10 min, the lid to the refuge was lifted from behind a blind via a pulley system and a 1 min acclimation period followed. After the lid was raised, the fish was allowed 10 min to explore the maze. From behind the blind, the observer viewed all of the trials and recorded the following behavioral metrics: refuge emergence time, the number of lines that were crossed within the maze (i.e., general activity patterns), and whether or not the fish reached the end of the maze. Following the Z-maze trial, the focal fish were moved into opaque Plexiglas isolation compartments ( $26.8 \times 9.2 \times 15.2$  cm, see McConnachie et al. 2012) that were maintained on independent aeration and a flow-through of fresh lake water (with water temperatures of  $24\text{--}26^\circ\text{C}$ ;  $\text{O}_2 > 90\%$  saturation) and were retained there for 2 h to allow recovery from any stressors that were associated with the maze trial experiment before the flight-initiation-distance test.

*The flight-initiation-distance test.*—The second behavioral test involved determining each focal fish's flight initiation distance (FID). This behavioral assay is widely used and standardized in teleosts for assessing an individual's

level of phenotypic boldness (Kim et al. 2009; Wilson et al. 2015; Cooke et al. 2017). The trials for FID were conducted in a large raceway-style tank ( $152.8 \times 27.4 \times 35.5$  cm) that consisted of opaque side and floor panels. The stimulus device consisted of a long plastic rod that was tipped with a novel object (a brightly colored orange and yellow fishing float). This float was comparable in size and color to those that were used in prior works (a simple orange ball) as a standardized means of conducting an FID trial (see Kim et al. 2009; Elvidge et al. 2013; Cooke et al. 2017; Prystay et al. 2017). This is a well-established methodological approach for conducting an FID trial. Graduations of 1 cm were marked along the edge of the tank to determine the flight distances. In between trials, water was circulated through the system to maintain the water parameters within a consistent range.

At the start of each trial, the focal fish was removed from the aforementioned isolation chamber and placed in the experimental arena, where it was allowed to acclimate in the tank for 2 min. During this time, the experimental observer, holding the stimulus device, was in plain sight and remained still. At the onset of the trial, the observer approached the fish with the stimulus device at a constant speed of 5 cm/s holding it an angle of approximately  $45^\circ$  to the fish. Using the measurements along the edge of the tank, the fish's flight response was measured as the distance (in cm) between the stimulus and the fish just before the fish darted away. Following the trial, the focal fish was then removed from the experimental arena and was weighed (OHAUS Valor 2000W scale, New Jersey, USA). All of the fish that were tested were released back to their point of origin. The caudal fin clips ensured that the individuals that were released were not subsequently used in additional experiments.

*Statistical analyses.*—The data were analyzed by using R Studio (version 3.2.3, R Core Team 2017), and the analyses were conducted by using the “pwr” package (Champerly 2018) and the “pscl” package for the zero-inflated Poisson model (Jackman 2017). Fish length and mass were correlated ( $r = 0.94$ ;  $P < 0.05$ ), so only length was included in the subsequent analyses to avoid overfitting. Three response variables, number of lines crossed, FID, and refuge emergence deviated from a normal distribution ( $P < 0.005$  for Shapiro–Wilk tests for all cases), so they were rank transformed to satisfy the normality assumption of parametric analyses (Scheirer et al. 1976). To account for multicollinearity, the behavioral measures (refuge emergence time, FID, and number of lines crossed) were combined and tested in one model by using a factorial MANCOVA against location (inside of the APA,  $n = 37$ ; inside of the transition zone,  $n = 35$ ; and outside of the APA,  $n = 36$ ), with fish length, fish parasite load, and temperature as covariates. The multivariate model was then separated to analyze each behavioral response variable

separately by using two ANCOVAs to explore how FID and refuge emergence time related to the same covariates as were in the previous analysis. Given that the number of lines crossed is count data and many fish did not cross any lines (value of 0), a zero-inflated Poisson model was used to explore the relationship between activity (not rank transformed) and the covariates (Jackman 2017). For all of the tests, differences were identified by using a Tukey post hoc analysis.

## RESULTS

Refuge emergence time did not differ between the fish that were obtained from the different source locations (Figure 2B), but the relationship between refuge emergence time and treatment was marginally nonsignificant for both the MANCOVA (Table 1) and the ANCOVA (Table 2). In contrast, the MANCOVA and the zero-inflated Poisson model comparing activity to treatment, temperature, body length, and parasite burden showed no relationship between the response variable and the covariates ( $P > 0.05$  for all cases;), regardless of the apparent higher activity level of the fish that were captured from outside of the

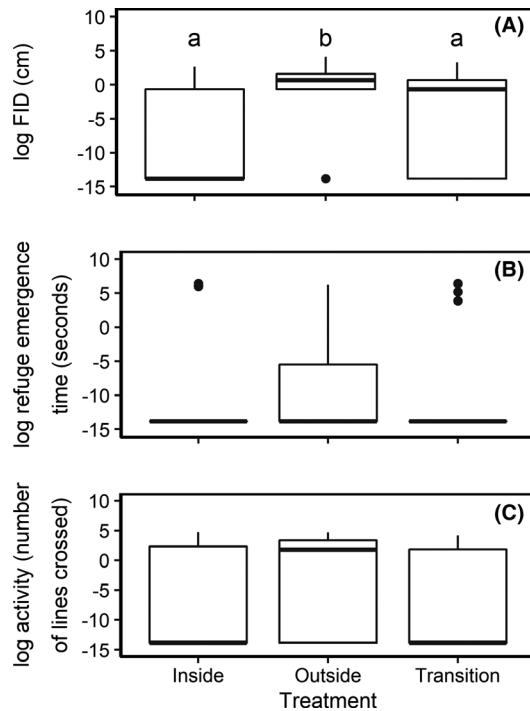


FIGURE 2. Boxplots showing Bluegill behavioral responses after being captured from inside the aquatic protected area (APA;  $n=37$ ), outside the APA ( $n=35$ ), and in the transition zone between the inside and outside of the APA ( $n=35$ ). Responses include (A) flight initiation distance (cm), (B) refuge emergence time (seconds), and (C) activity (number of lines crossed). Significant differences are identified with letters. Values were considered significant at  $\alpha < 0.05$ .

TABLE 1. Summary of the factorial MANCOVA examining the fish behavioral responses (flight initiation distance (m), activity (number of lines crossed), and refuge emergence [seconds]). Values were considered significant at  $\alpha < 0.05$ , and significant  $P$ -values are denoted in bold italics.

Response	$F$	$P$
<b>Treatment (df = 2, n = 107)</b>		
FID	11.15	<b>&lt;0.001</b>
Activity	1.61	0.20
Refuge emergence	2.58	0.080
<b>Temperature (df = 1, n = 107)</b>		
FID	1.27	0.26
Activity	0.92	0.34
Refuge emergence	0.075	0.79
<b>Length (df = 1, n = 107)</b>		
FID	0.33	0.57
Activity	0.78	0.38
Refuge emergence	0.0090	0.92
<b>Parasite (df = 1, n = 107)</b>		
FID	1.14	0.29
Activity	1.69	0.20
Refuge emergence	0.47	0.49

TABLE 2. Summary of the two ANCOVA outputs comparing flight initiation distance (m) and refuge emergence time to treatments (i.e., capture site), temperature, fish length, and fish parasite load. Both response variables (FID and refuge emergence) were rank transformed to account for the deviation from normal distribution in the data. Values were considered significant at  $\alpha < 0.05$ , and significant  $P$ -values are denoted in bold italics.

Response	Covariates	df	$F$	$P$
Rank(FID)	Population	2	11.15	<b>&lt;0.001</b>
	Temperature	1	1.27	0.26
	Length	1	0.33	0.59
	Parasite	1	1.14	0.29
Rank(Emergence time)	Population	2	2.59	0.080
	Temperature	1	0.075	0.79
	Length	1	0.0090	0.92
	Parasite	1	0.47	0.49

APA compared with that of those in the other treatments (Figure 2C).

For both the factorial MANCOVA (Table 1), where the behavioral response data were combined, and the ANCOVAs (Table 2), where the behavioral response variables were analyzed separately, only the source of the fish had an effect on FID. More specifically, the Tukey post hoc analysis showed that FID for the fish that were captured outside of the APA was significantly higher than that for those that were captured inside of the APA

( $P < 0.001$ ) or in the transition zone ( $P = 0.019$ ). However, FID for the fish from outside of the APA was only slightly higher than it was for the fish from the transition zone and inside of the APA (0.52 cm and 2.34 cm, respectively [Figure 2A]). There was no significant difference in FID between the fish that were captured from the transition zone and those that were caught inside of the APA ( $P = 0.14$ ).

## DISCUSSION

We tested the hypothesis that fish that were obtained from main lake habitats (i.e., those subject to fishing) would exhibit more timid behavioral phenotypes than those that were obtained from the APA, as a direct result of fishing mortality selecting against bold individuals (e.g., Arlinghaus et al. 2017; Lennox et al. 2017). However, our findings suggest a mixed effect of APAs on the behavioral phenotypes of fish. Indeed, the results from the Z-maze and FID trials contradict one another, with APAs seemingly having a null or directional effect, respectively, on phenotypic traits that are associated with the bold–shy continuum in Bluegill. This was unexpected because it is believed that fishing mortality removes bold phenotypes and thus leads to a population with more timid individuals (e.g., Alós et al. 2012; Arlinghaus et al. 2017). We were expecting to observe greater FIDs, reduced refuge emergence times, and higher bouts of activity and exploratory activities in the fish that were sourced from APAs, which are all metrics that are associated with a bolder behavioral phenotype (Toms et al. 2010; Conrad et al. 2011) and are important components of risk-taking-related decision making (Lima and Dill 1990). Indeed, bolder individuals are typically more susceptible to capture by fisheries, especially those that involve hook and line and trap entry, and these two fisheries gears are used in Lake Opinicon (Wilson et al. 1993, 2015; Alós et al. 2012; Sutter et al. 2012; and reviewed in Arlinghaus et al. 2017). This acts to restructure the local populations, from a behavioral perspective, in a directional manner (Lennox et al. 2017). Therefore, we anticipated that there would be a more consistent signature of the lake's APA associated with the behavioral traits that were explored here, especially given that centrarchid fishes are subject to the effects of both fishing mortality and FIE at broader scales (Cooke et al. 2007; Philipp et al. 2009; Wilson et al. 2015).

The only prior work that has addressed the role of APAs on boldness/exploratory parameters in centrarchid fishes was conducted by Cooke et al. (2017). These authors found no influence of APAs on the exploratory and risk-taking behaviors of Largemouth Bass or on their activity patterns relative to fish that were sourced from the fished areas in the lake. While this is similar to our findings, with respect to the Z-maze trial, this is a generally

data-deficient area where more investigation is needed. However, there does appear to be a difference in behavioral traits between fish that are sourced from the APA and those from the main lake with respect to the FID trials. The Bluegill that were sampled from the main lake population exhibited a behavioral phenotype that was more timid than those from the APA and transitional populations, which was indicated by higher FID scores, an effect that is consistent with reports in the literature (Gotanda et al. 2009; Feary et al. 2011; Januchowski-Hartley et al. 2011; Rhoades et al. 2018). Our FID data does suggest that these APA and non-APA areas are under differential selection forces, which may be attributable to differences in angling-related pressures.

This mixed effect of APAs on the behavioral dynamics of Bluegill may result from several factors. It could be that fisheries activities are acting selectively on particular traits that are associated with risk-taking, boldness, and general exploratory/activity patterns. While information concerning population-level behavioral trait selection under differential fisheries pressures is rather scant, previous work on Largemouth Bass supports this notion. Cooke et al. (2017) found that angled Largemouth Bass that were obtained from both heavily fished and protected populations exhibited comparable refuge emergence timing and FID scores, suggesting little action for FIE in modulating the behavioral dynamics, in this particular context, of this species at the population level. However, given that other behavioral traits that are associated with boldness in Largemouth Bass appear to be influenced by APAs, including overall aggression scores and lure strikes per cast (e.g., Twardek et al. 2017), alterations in behavioral phenotypes that are associated with APAs appear to be highly context dependent, with only a certain subset of behavioral traits/characteristics that are associated with the shy–bold continuum being under selection (Wilson et al. 2011). Indeed, previous works that have addressed the role of APAs in affecting population-level behavioral traits appear to have found a null effect in a number of behavioral characteristics that are associated with boldness in teleosts (e.g., Binder et al. 2012; Kekäläinen et al. 2014; Cooke et al. 2017). Therefore, the comparable behavioral phenotypes that were exhibited by the Bluegill from the three locations in the lake may simply represent a lack of selection for these traits in a fisheries-related context. However, we exercise a degree of caution in this, as boldness–angling vulnerability relationships can be nonexistent under certain circumstances wherein selective pressures may be unable to exert an effect on the local population of fish (Vainikka et al. 2016). For example, while Yellow Perch *Perca flavescens* exhibited variation in boldness scores (including exploratory metrics, freezing responses, and spatial use patterns) in response to a predator, these traits did not relate to the individual's susceptibility to an

angling event (Vainikka et al. 2016). In this case, APAs may not alter the behavioral phenotype of a population of fish. It is also possible (and likely) that there is some level of mixing between fish from the different areas in the lake. Additionally, we cannot discredit the role of our collection methods in biasing our study population towards having a greater proportion of bolder individuals (Wilson et al. 2011), which possibly resulted in behavioral homogeneity between our three lake populations. Indeed, Wilson et al. (2011) found that individual Bluegill that were caught on rod and reel were, on average, consistently bolder than individuals that were caught by using passive gear types such as seine nets. This may have led to biases within our data set because we only used angling to capture our fish. While we were constrained in our fish collection methodology (i.e., we used rod and reel), further work should include the use of less biased collection procedures, such as seining (e.g., see Lawrence et al. 2018, 2019). Lastly, we acknowledge that CPUE in the various capture sites was not characterized in our study and may add uncertainty in our conclusions. As APAs have been shown to have higher CPUEs than do surrounding waters (e.g., Kaunda-Arara and Rose 2004; Goñi et al. 2006; Vandepierre et al. 2011), we may have expected that APAs in the Lake Opinicon system could experience a similar effect that could have influenced our results. Furthermore, as CPUE is often considered a factor of abundance (Hinton and Maunder 2003; Haggarty and King 2006; Tsuboi and Endou 2008) and that both abundance and biomass of Bluegill is comparable across our study regions in this particular lake (Zolderdo et al. 2019), we might not have expected any significant influence of the APA on CPUE in this study. Nonetheless, we urge caution when interpreting these findings.

The effects of APAs on fish behavior appear to have a temporal aspect with respect to their history. Indeed, it has been shown empirically that several species of teleosts from a kelp forest in California that were obtained from long-standing APAs (~40–100 years old) had shorter flight distances and demonstrated bolder behavioral phenotypes than did those from newly formed APAs (7 years old; Rhoades et al. 2018). As was proposed by Philipp et al. (2009), boldness traits in fish that are related to angling vulnerability are heritable such that fishing mortality has the potential to select for populations in APAs that are bolder than those in unprotected sites. If APAs conserve bold behavioral phenotypes, it is likely that these fish will also have greater foraging success, higher energy gains, and increased fitness, which has the potential to boost or maintain population productivity (Réale et al. 2000; Biro and Post 2008). These ecological benefits, though not examined in this study, would be beneficial to investigate to determine the full effects that the APA has had upon the Bluegill population in Lake

Opinicon. Additionally, it is important to realize that fleeing from a supposed predator and the traits that are associated with predator avoidance (e.g., flight trajectory, timing and speed, swimming duration, inspection behaviors, etc.), in the context of bold–shy continuum, represent a sum of both genetic/innate factors and learned behaviors (Godin 1997; Smith 1997). Indeed, the factors that we have highlighted above that are associated with the general flight response do appear to be affected by APAs/fisheries mortality (Bergseth et al. 2016). Consequently, alterations that are associated with risk-taking under circumstances where differential population structuring that is associated with APAs may be present could then represent both a selection aspect that is associated with fishing mortality (i.e., FIE) and a learned fear of human activity (e.g., Côté et al. 2014), which would be difficult to tease apart by using our current experimental design. Furthermore, given that bold–shy patterns can influence ecological interactions such as predator–prey dynamics (e.g., Harris et al. 2010; Smith and Blumstein 2010; Elvidge et al. 2014), it would be of great interest to investigate the secondary effects of anthropogenic activities in this context as they relate to whole ecosystem functioning and dynamics. This could be a useful tool for addressing shifts within the structure of a fish population and observing shifts within the community and ecosystem. Additionally, it is important to realize that predation risk may have had a role in affecting which individuals were captured during specimen collection such that timid animals may have been reluctant to take our baited hooks and thus potentially served as an experimental bias. This may be particularly important in APAs where predator abundances may differ between fished and nonfished reaches (e.g., Kruschel et al. 2012; Hackradt et al. 2014; Zolderdo et al. 2019). Although, this seems unlikely given that the relatively large Bluegill that were used in this experiment (~13 cm TL) are generally free from predation by aquatic piscivores (mainly Large-mouth Bass) and prior work has demonstrated a size-dependent perception of risk in sunfishes (Werner et al. 1983; Werner and Hall 1988; Shoup et al. 2003; Lawrence et al. 2018, 2019) such that behavioral modifications in the presence of predation risk are minimal (Werner and Hall 1988; Shoup et al. 2003), with a corresponding low risk of predator mortality (Werner and Hall 1988; Hill et al. 2004). While this is speculative, further work should be conducted to assess the relative effect that perceived predation risk may have on skewing the behavioral phenotypes of collected focal fish. Overall, our findings suggest that APAs may be an effective approach for maintaining diverse behavioral phenotypes in exploited systems and are thus consistent with the idea of evolutionarily enlightened management (Ashley et al. 2003; Cook and Sgrò 2017).

## ACKNOWLEDGMENTS

We would like to thank the Queens University Biological Station staff for facilitating this research. We also thank an anonymous reviewer for their helpful comments on this manuscript. Emily N. Moynes and Michael J. Lawrence are co-first authors. There is no conflict of interest declared in this article.

## ORCID

Michael J. Lawrence  <https://orcid.org/0000-0002-4801-1580>

Aaron J. Zolderdo  <https://orcid.org/0000-0003-1588-565X>

Steven J. Cooke  <https://orcid.org/0000-0002-5407-0659>

## REFERENCES

- Allan, J. D., R. Abell, Z. E. B. Hogan, C. Revenga, B. W. Taylor, R. L. Welcomme, and K. Winemiller. 2005. Overfishing of inland waters. *BioScience* 55:1041–1051.
- Alós, J., M. Palmer, and R. Arlinghaus. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. *PLoS (Public Library of Science) ONE [online serial]* 7:e48030.
- Alós, J., M. Palmer, P. Trias, C. Díaz-Gil, and R. Arlinghaus. 2014. Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. *Canadian Journal of Fisheries and Aquatic Sciences* 72:217–225.
- Alós, J., A. Puiggrós, C. Díaz-Gil, M. Palmer, R. Rosselló, and R. Arlinghaus. 2015. Empirical evidence for species-specific export of fish naïveté from a no-take marine protected area in a coastal recreational hook and line fishery. *PLoS (Public Library of Science) ONE [online serial]* 10:e0135348.
- Arlinghaus, R., K. L. Laskowski, J. Alós, T. Klefoth, C. T. Monk, S. Nakayama, and A. Schröder. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18:360–373.
- Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O. Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionarily enlightened management. *Biological Conservation* 111:115–123.
- Barber, I., D. Hoare, and J. Krause. 2000. Effects of parasites on fish behavior: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries* 10:131–165.
- Baskett, M. L., S. A. Levin, S. D. Gaines, and J. Dushoff. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. *Ecological Applications* 15:882–901.
- Bergseth, B. J., D. H. Williamson, A. J. Frisch, and G. R. Russ. 2016. Protected areas preserve natural behavior of a targeted fish species on coral reefs. *Biological Conservation* 198:202–209.
- Binder, T. R., M. A. Nannini, D. H. Wahl, R. Arlinghaus, T. Klefoth, D. P. Philipp, and S. J. Cooke. 2012. Largemouth Bass selected for differential vulnerability to angling exhibit similar routine locomotory activity in experimental ponds. *Transactions of the American Fisheries Society* 141:1252–1259.
- Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the USA* 105:2919–2922.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509–515.
- Burns, C. 2007. Biological sustainability of commercial fishing in the inland waters of Kemptville District. Ontario Ministry of Natural Resources, Technical Paper, Kemptville.
- Champany, S. 2018. pwr: basic functions for power analysis. R Core Team, Vienna.
- Chapman, B. B., L. J. Morrell, and J. Krause. 2010. Unpredictability in food supply during early life influences boldness in fish. *Behavioral Ecology* 21:501–506.
- Conrad, J. L., K. L. Weinersmith, T. Brodin, J. B. Saltz, and A. Sih. 2011. Behavioral syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology* 78:395–435.
- Cook, C. N., and C. M. Sgrò. 2017. Aligning science and policy to achieve evolutionarily enlightened conservation. *Conservation Biology* 31:501–512.
- Cooke, S. J., and I. G. Cowx. 2004. The role of recreational fishing in global fish crises. *BioScience* 54:857–859.
- Cooke, S. J., C. D. Suski, K. G. Ostrand, D. H. Wahl, and D. P. Philipp. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* 80:480–490.
- Cooke, E. L., A. D. Wilson, C. K. Elvidge, and S. J. Cooke. 2017. Does capture method or the presence of aquatic protected areas influence the selective harvest of behavioral types in Largemouth Bass? *Canadian Journal of Fisheries and Aquatic Sciences* 74:1151–1157.
- Côté, I. M., E. S. Darling, L. Malpica-Cruz, N. S. Smith, S. J. Green, J. Curtis-Quick, and C. Layman. 2014. What doesn't kill you makes you wary? Effect of repeated culling on the behavior of an invasive predator. *PLoS (Public Library of Science) ONE [online serial]* 9:e94248.
- Diaz Puali, B., and A. Sih. 2017. Behavioral responses to human-induced change: why fishing should not be ignored. *Evolutionary Ecology* 10:231–240.
- Elvidge, C. K., C. J. Macnaughton, and G. E. Brown. 2013. Sensory complementation and antipredator behavioral compensation in acid-impacted juvenile Atlantic Salmon. *Oecologia* 172:69–78.
- Elvidge, C. K., I. Ramnarine, and G. E. Brown. 2014. Compensatory foraging in Trinidadian guppies: effects of acute and chronic predation threats. *Current Zoology* 60:323–332.
- Feary, D. A., J. E. Cinner, N. A. Graham, and F. A. Januchowski-Hartley. 2011. Effects of customary marine closures on fish behavior, spear-fishing success, and underwater visual surveys. *Conservation Biology* 25:341–349.
- Godin, J.-G. J. 1997. Evading predators. Pages 191–226 in J.-G. J. Godin, editor. *Behavioral ecology of teleost fishes*. Oxford University Press, Oxford, UK.
- Goñi, R., A. Quetglas, and O. Reñones. 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Marine Ecology Progress Series* 308:207–219.
- Gotanda, K. M., K. Turgeon, and D. L. Kramer. 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. *Behavioral Ecology and Sociobiology* 63:1563–1572.
- Haggarty, D. R., and J. R. King. 2006. CPUE as an index of relative abundance for nearshore reef fishes. *Fisheries Research* 81:89–93.
- Hackradt, C. W., J. A. García-Charton, M. Harmelin-Vivien, A. Perez-Ruzafa, L. Le Direach, J. Bayle-Sempere, E. Charbonnel, D. Ody, O. Renones, P. Sanchez-Jerez, and C. Valle. 2014. Response of rocky reef top predators (Serranidae: Epinephelinae) in and around marine protected areas in the western Mediterranean Sea. *PLoS (Public Library of Science) ONE [online serial]* 9:e98206.
- Härkönen, L., P. Hyvärinen, J. Paappanen, and A. Vainikka. 2014. Explorative behavior increases vulnerability to angling in hatchery-



- reared Brown Trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 71:1900–1909.
- Harris, S., I. W. Ramnarine, H. G. Smith, and L. B. Pettersson. 2010. Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. Oikos 119:1711–1718.
- Harrison, I. J., P. A. Green, T. A. Farrell, D. Juffe-Bignoli, L. Sáenz, and C. J. Vörösmarty. 2016. Protected areas and freshwater provisioning: a global assessment of freshwater provision, threats and management strategies to support human water security. Aquatic Conservation: Marine and Freshwater Ecosystems 26:103–120.
- Heino, M., L. Baulier, D. S. Boukal, B. Ernande, F. D. Johnston, F. M. Mollet, H. Pardoe, N. O. Therkildsen, S. Uusi-Heikkilä, A. Vainikka, R. Arlinghaus, D. J. Dankel, E. S. Dunlop, A. M. Eikeset, K. Enberg, G. H. Engelhard, J. Jørgensen, A. T. Laugen, S. Matsumura, S. Nusslé, D. Urbach, R. Whitlock, A. D. Rijnsdorp, and U. Dieckmann. 2013. Can fisheries-induced evolution shift reference points for fisheries management? ICES (International Council for the Exploration of the Sea) Journal of Marine Science 70:707–721.
- Heino, M., B. Diaz Pauli, and U. Dieckmann. 2015. Fisheries-induced evolution. Annual Review of Ecology, Evolution, and Systematics 46:461–480.
- Heino, M., and O. R. Godø. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70:639–656.
- Hill, J. E., L. G. Nico, C. E. Clchra, and C. R. Gilbert. 2004. Prey vulnerability to Peacock Cichlids and Largemouth Bass based on predator gape and prey body depth. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 58:47–56.
- Hinton, M. G., and M. N. Maunder. 2004. Methods for standardizing CPUE and how to select among them. Collective Volume of Scientific Papers ICCAT 56:169–177.
- Hollins, J., D. Thambithurai, B. Koeck, A. Crespel, D. M. Bailey, S. J. Cooke, J. Lindstrom, K. J. Parsons, and S. S. Killen. 2018. A physiological perspective on fisheries-induced evolution. Evolutionary Applications 11:561–576.
- Hutchings, J. A. 2009. Avoidance of fisheries-induced evolution: management implications for catch selectivity and limit reference points. Evolutionary Applications 2:324–334.
- Ioannou, C. C., M. Payne, and J. Krause. 2008. Ecological consequences of the bold–shy continuum: the effect of predator boldness on prey risk. Oecologia 157:177–182.
- Jackman, S. 2017. Package ‘pscl.’ Available: <http://github.com/atahk/pscl>. (December 2019).
- Januchowski-Hartley, F. A., N. A. Graham, D. A. Feary, T. Morove, and J. E. Cinner. 2011. Fear of fishers: human predation explains behavioral changes in coral reef fishes. PLoS (Public Library of Science) ONE [online serial] 6:e22761.
- Kaunda-Arara, B., and G. A. Rose. 2004. Effects of marine reef National Parks on fishery CPUE in coastal Kenya. Biological Conservation 118:1–13.
- Kekäläinen, J., T. Podgorniak, T. Puolakka, P. Hyvärinen, and A. Vainikka. 2014. Individually assessed boldness predicts *Perca fluviatilis* behavior in shoals, but is not associated with the capture order or angling method. Journal of Fish Biology 85:1603–1616.
- Kim, J. W., G. E. Brown, I. J. Dolinsek, N. N. Brodeur, A. O. Leduc, and J. W. Grant. 2009. Combined effects of chemical and visual information in eliciting antipredator behavior in juvenile Atlantic Salmon *Salmo salar*. Journal of Fish Biology 74:1280–1290.
- Kobler, A., G. E. Maes, Y. Humblet, F. A. Volckaert, and M. Eens. 2011. Temperament traits and microhabitat use in bullhead, *Cottus perifretum*: fish associated with complex habitats are less aggressive. Behaviour 148:603–625.
- Kruschel, C., S. T. Schultz, T. Bakran-Petricioli, and D. Petricioli. 2012. Comparing predator abundance and fish diversity in MPA sites (Kornati NP, Croatia) and adjacent sites exploited by fisheries. Croatian Journal of Fisheries 70:S65–S78.
- Kuparinen, A., and J. Merilä. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology and Evolution 22:652–659.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8:S72–S78.
- Lawrence, M. J., J. G. J. Godin, and S. J. Cooke. 2018. Does experimental cortisol elevation mediate risk-taking and antipredator behavior in a wild teleost fish? Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 226:75–82.
- Lawrence, M. J., J. G. J. Godin, A. J. Zoldero, and S. J. Cooke. 2019. Chronic plasma cortisol elevation does not promote riskier behavior in a teleost fish: a test of the behavioral resiliency hypothesis. Integrative Organismal Biology 1:obz009.
- Lennox, R. J., J. Alós, R. Arlinghaus, A. Horodysky, T. Klefoth, C. T. Monk, and S. J. Cooke. 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish and Fisheries 18:986–1010.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.
- McConnachie, S. H., C. M. O'Connor, K. M. Gilmour, G. K. Iwama, and S. J. Cooke. 2012. Supraphysiological cortisol elevation alters the response of wild Bluegill Sunfish to subsequent stressors. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 317:321–332.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Bratney, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935.
- Ontario Department of Game and Fisheries. 1946. Annual Report, 1935–1946. Game and Fisheries Department, Toronto.
- Ontario Ministry of Natural Resources. 1995. 1994 creel summaries for Opinicon and Sydenham Lakes. Ontario Ministry of Natural Resources, Rideau Lakes Fisheries Assessment Unit, File Report 1995-1, Sharbot Lake.
- Ontario Ministry of Natural Resources and Forestry. 2015. 2010 survey of recreational fishing in Canada: results for fisheries management zones of Ontario. Ontario Ministry of Natural Resources and Forestry, Peterborough.
- Oswald, M. E., R. E. Drew, M. Racine, G. K. Murdoch, and B. D. Robison. 2012. Is behavioral variation along the bold-shy continuum associated with variation in the stress axis in Zebrafish? Physiological and Biochemical Zoology 85:718–728.
- Oswald, M. E., M. Singer, and B. D. Robison. 2013. The quantitative genetic architecture of the bold-shy continuum in Zebrafish, *Danio rerio*. PLoS (Public Library of Science) ONE [online serial] 8:e68828.
- Philipp, D. P., J. E. Claussen, J. B. Koppelman, J. A. Stein, S. J. Cooke, C. D. Suski, D. H. Wahl, D. A. H. Sutter, and R. Arlinghaus. 2015. Fisheries-induced evolution in Largemouth Bass: linking vulnerability to angling, parental care, and fitness. Pages 223–234 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.
- Philipp, D. P., S. J. Cooke, J. E. Claussen, J. B. Koppelman, C. D. Suski, and D. P. Burkett. 2009. Selection for vulnerability to angling in Largemouth Bass. Transactions of the American Fisheries Society 138:189–199.
- Prystay, T. S., C. K. Elvidge, W. M. Twardek, J. M. Logan, C. H. Reid, S. H. Clarke, J. G. Foster, E. L. L. Cooke, and S. J. Cooke. 2017. Comparison of the behavioral consequences and recovery patterns of

- Largemouth Bass exposed to MS-222 or electrosedation. *Transactions of the American Fisheries Society* 146:556–566.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: <https://www.R-project.org/>. (December 2019).
- Réale, D., B. Y. Gallant, M. Leblanc, and M. Festa-Bianchet. 2000. Consistency of temperament in bighorn ewes and correlates with behavior and life history. *Animal Behavior* 60:589–597.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Rhoades, O. K., S. I. Lonhart, and J. J. Stachowicz. 2018. Fished species uniformly reduced escape behaviors in response to protection. *Biological Conservation* 226:238–246.
- Scheirer, C. J., W. S. Ray, and N. Hare. 1976. The analysis of ranked data derived from completely randomized factorial designs. *Biometrics* 32:429–434.
- Shoup, D. E., R. E. Carlson, and R. T. Heath. 2003. Effects of predation risk and foraging return on the diel use of vegetated habitat by two size-classes of Bluegills. *Transactions of the American Fisheries Society* 132:590–597.
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioral syndromes. *Ecology Letters* 15:278–289.
- Smith, R. J. F. 1997. Avoiding and deterring predators. Pages 163–190 in J.-G. J. Godin, editor. *Behavioral ecology of teleost fishes*. Oxford University Press, Oxford, UK.
- Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19:448–455.
- Smith, B. R., and D. T. Blumstein. 2010. Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behavioral Ecology* 21:919–926.
- Suski, C. D., and S. J. Cooke. 2007. Conservation of aquatic resources through the use of freshwater protected areas: opportunities and challenges. *Biodiversity and Conservation* 16:2015–2029.
- Suski, C. D., and D. P. Philipp. 2004. Factors affecting the vulnerability to angling of nesting male Largemouth and Smallmouth bass. *Transactions of the American Fisheries Society* 133:1100–1106.
- Sutter, D. A., C. D. Suski, D. P. Philipp, T. Klefoth, D. H. Wahl, P. Kersten, S. J. Cooke, and R. Arlinghaus. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences of the USA* 109:20960–20965.
- Thomson, J. S., P. C. Watts, T. G. Pottinger, and L. U. Sneddon. 2011. Physiological and genetic correlates of boldness: characterising the mechanisms of behavioral variation in Rainbow Trout *Oncorhynchus mykiss*. *Hormones and Behavior* 59:67–74.
- Toms, C. N., D. J. Echevarria, and D. J. Jouandot. 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology* 23:1–25.
- Tsuboi, J. I., and S. Endou. 2008. Relationships between catch per unit effort, catchability, and abundance based on actual measurements of salmonids in a mountain stream. *Transactions of the American Fisheries Society* 137:496–502.
- Twardek, W. M., C. K. Elvidge, A. D. Wilson, D. A. Algera, A. J. Zolderdo, S. C. Loughheed, and S. J. Cooke. 2017. Do protected areas mitigate the effects of fisheries-induced evolution on parental care behavior of a teleost fish? *Aquatic Conservation: Marine and Freshwater Ecosystems* 27:789–796.
- Uusi-Heikkilä, S., C. Wolter, T. Klefoth, and R. Arlinghaus. 2008. A behavioral perspective on fishing-induced evolution. *Trends in Ecology and Evolution* 23:419–421.
- Vandeperre, F., R. M. Higgins, J. Sánchez-Meca, F. Maynou, R. Goñi, P. Martín-Sosa, A. Pérez-Ruzafa, P. Afonso, I. Bertocci, R. Crechriou, G. D'Anna, M. Dimech, C. Dorta, O. Esparza, J. M. Falcón, A. Forcada, I. Guala, L. Le Direach, C. Marcos, C. Ojeda-Martínez, C. Pipitone, P. J. Schembri, V. Stelzenmüller, B. Stobart, and R. S. Santos. 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. *Fish and Fisheries* 12:412–426.
- Vainikka, A., I. Tammela, and P. Hyvärinen. 2016. Does boldness explain vulnerability to angling in Eurasian Perch *Perca fluviatilis*? *Current Zoology* 62:109–115.
- Warren, M. L. 2009. Centrarchid identification and natural history. Pages 375–534 in S. J. Cooke and D. P. Phillip, editors. *Centrarchid fishes: diversity, biology, and conservation*. Blackwell Publishing, West Sussex, UK.
- Watson, D. L., E. S. Harvey, G. A. Kendrick, K. Nardi, and M. J. Anderson. 2007. Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. *Marine Biology* 152:1197–1206.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in Bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366.
- Westera, M., P. Lavery, and G. Hyndes. 2003. Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. *Journal of Experimental Marine Biology and Ecology* 294:145–168.
- Wilson, A. D., T. R. Binder, K. P. McGrath, S. J. Cooke, and J. G. J. Godin. 2011. Capture technique and fish personality: angling targets timid Bluegill sunfish, *Lepomis macrochirus*. *Canadian Journal of Fisheries and Aquatic Sciences* 68:749–757.
- Wilson, A. D., J. W. Brownscombe, B. Sullivan, S. Jain-Schlaepfer, and S. J. Cooke. 2015. Does angling technique selectively target fishes based on their behavioral type? *PLoS (Public Library of Science) ONE [online serial]* 10:e0135848.
- Wilson, D. S., A. B. Clark, K. Coleman, and T. Dearstyne. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution* 9:442–446.
- Wilson, D. S., K. Coleman, A. B. Clark, and L. Biederman. 1993. Shy-bold continuum in Pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology* 107:250.
- Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution* 27:452–461.
- Zolderdo, A. J., A. E. Abrams, C. H. Reid, C. D. Suski, J. D. Midwood, and S. J. Cooke. 2019. Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29:1106–1122.